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Predation by wolves and other large carnivores in northwestern Montana and southeastern British Columbia

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PREDATION BY WOLVES
AND OTHER LARGE CARNIVORES IN NORTHWESTERN MONTANA
AND SOUTHEASTERN BRITISH COLUMBIA

by

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B.S. South Dakota State University, 1987

M.S. University of Minnesota, 1992

presented in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy
University of Montana
1997

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Predation by Wolves and other Large Carnivores in Northwestern Montana and Southeastern British Columbia (272 pp.)

DHP
Director: Daniel H. Pletscher

Few researchers have simultaneously and intensively examined both predators and prey in multi-predator, multi-prey systems. Therefore, I examined relationships between wolves (*Canis lupus*) and white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and moose (*Alces alces*) in the North Fork of the Flathead Basin from 1992-1996. I also compared patterns of prey selection among wolves, cougars (*Puma concolor*), and humans to ascertain the effects of wolf recolonization and multiple predators on prey and on each other. White-tailed deer made up the greatest proportion of both wolf (0.83) and cougar (0.87) diets, but elk and moose made up a larger proportion of wolf (0.14, 0.03, respectively) than cougar (0.06, 0.02, respectively) diets. Wolves and cougars selected similar age and sex classes in both deer and elk.

Annual survival rates were 0.74, 0.83, and 0.88 for deer, elk, and moose, respectively. Cougars and wolves were the most significant source of mortality for deer and elk and wolves and bears were the most significant source of mortality for moose. Deer and elk population declines were positively correlated with wolf numbers. The moose population remained mostly stable. Predation appeared to be the major factor limiting deer and elk populations in this system.

Wolves selected to hunt in white-tailed deer winter ranges and within these areas they selected to kill elk and moose over deer. Snow depth was positively correlated with and best explained the variation in proportion of deer selected by wolves annually. Snow depth and wolf density were positively correlated with and explained most of the annual variation in the total kill rate of wolves. Proportion of deer selected by wolves explained most of the annual variation in kill rate per wolf.

Wolves killed deer in areas with greater hiding/stalking cover and less slope than was available on wolf travel routes. Wolves killed deer at sites with less slope, fewer mature trees, and less canopy coverage than was present at sites where cougars killed deer. Five of 10 radiocollared deer used areas with denser canopy cover in the presence of wolves than they did in the absence of wolves.

PREFACE

In 1986, the University of Montana in cooperation with the U.S. Fish and Wildlife Service, the U.S. National Park Service, and the U.S. Forest Service began studying wolves that had begun to recolonize northwestern Montana. I began my PhD research on predation ecology of wolves as part of this effort in 1992. Concurrently, the Hornocker Wildlife Institute (HWI) began to study cougar ecology in the same study area. We began both of these projects as a truly collaborative research effort aimed at examining the effects of wolves and cougars on each other and on their prey base. This cooperative research effort resulted in a much more comprehensive examination of carnivore predation ecology in our study area.

The following dissertation is composed of 5 manuscripts (chapters) generated primarily from my field work examining wolf predation ecology. Chapter 1 is a product of the cooperative research with HWI. Hornocker Wildlife Institute project personnel captured and radio and backtracked the cougars. Kills they discovered as a result of this were incorporated in my sample of cougar and wolf kills. Toni Ruth and Maurice Hornocker (HWI) will be co-authors on this manuscript when it is submitted. Chapter 2 incorporates data collected on 3 master's projects done on deer, elk, and moose at the University of Montana by Jon Rachael, Mike MacLeod, and Meg Langley prior to my arrival. Chapter 3 also greatly benefits from the collaboration with HWI in that they collected data at cougar kill sites they discovered. Chapter 4 incorporates wolf backtracking data collected by Mike Fairchild, Diane Boyd, and Bob Ream from 1986-1992. Chapter 5 relies heavily on field work coordinated by Wendy Clark after I had left the study area to begin data analysis and she will be co-author on this manuscript when it is submitted. Because of all of this, "we" instead of "I" is used throughout the dissertation. I did all the data analysis and writing and take full responsibility for any errors contained in this dissertation.

We followed protocols approved by the University of Montana and University of Idaho Animal Care and Use Committees.

TABLE OF CONTENTS

TABLE OF CONTENTS (cont'd)

TABLE OF CONTENTS (cont'd)

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 5

ACKNOWLEDGEMENTS

We appreciate financial support from the U.S. Fish and Wildlife Service; National Park Service; Intermountain Research Station, U.S. Forest Service; British Columbia Wildlife Branch, Montana Dept. of Fish, Wildlife and Parks; McIntire-Stennis Program at the School of Forestry, University of Montana; Montana Cooperative Wildlife Research Unit; Rocky Mountain Elk Foundation; Peter W. Busch Family Foundation; Richard King Mellon Foundation; G. C. Hixon; and the National Geographic Society.

We appreciate the important field help and logistical support provided by Scott Emmerich and Regi Altop of the North Fork Subdistrict of Glacier National Park, more importantly, we appreciate their hospitality, warm meals, and friendship. We were able to classify cause of death for many kills mainly due to the commitment and extra efforts of these 2 rangers. Allie Wood (GNP trail crew leader extaordinaire) assisted us in the field and provided food, beer, friendship and warmth during all seasons.

Mike MacLeod, Jon Rachael, and Meg Langley provided valuable advice and made their data readily available. Bob Ream, Diane Boyd, Ed Bangs, Joe Fontaine, Steve Fritts, Jim Tilmant, Bruce Hird, Steve Gniadek, Brace Hayden, Harvey Nyberg, Tim Thier, Jim Cross, and Anna Fontana, provided valuable advice, encouragement, and field support. My dissertation committee members, Erick Greene, Bob Ream, Les Marcum, Jack Lyon, and Hans Zuuring provided thorough critiques of my study plan and dissertation. Jiri Doskocil and Peter Singleton greatly aided in GIS analysis. Jeanne Franz, Margaret Bachmeier, and Laura Plute cheerfully and efficiently carried out clerical and technical duties related to the project.

I have had the truly good fortune of working with 2 of the most committed wildlife professionals in the field on my graduate projects. I thought it was going to be very difficult to find another advisor as exceptional and as hard-working as Dave Mech, but Dan Pletscher certainly was just that. Dan excelled in everything I think an advisor should be and was truly fun to work with. Like very few, Dan wears the hat of teacher, researcher, and administrator equally well.

I believe the collaboration and cooperation that developed between this project and the Hornocker Wildlife Institute cougar project is a model for many other ventures that might and should be considered. As a result we were able to collect much more data and provide a much more complete picture of the large mammal predator/prey system of the North Fork. I thank Maurice Hornocker, Howard Quigley and HWI field personnel including Jamie Jonkel, Tom Parker, Randy Siemens, and Clint Gray. I don't think I could have found a better field colleague than Toni Ruth; she added

greatly to the joy of life in the North Fork and has become a great friend. Many parts of this dissertation result from the help and advice of her and her field crew.

My study also benefitted greatly from collaboration and cooperation with Wendy Arjo who started conducting PhD research on coyotes in the North Fork in 1994. The coyote project and my project worked together trapping wolves, locating radiocollared animals, and examining kills. Wendy too has become a valued friend during this effort.

We were very privileged to live and work in what is increasingly becoming hard to find; a true community. The residents of.the North Fork reminded me of the importance of neighbors, and my work and stay in the North Fork was enriched by all of them that I met. I especially appreciate the friendship, hospitality, help and private property access of Larry Wilson, John and Pat Elliot, Barbara Klempnow, Tom and Joan Ladenburg, Lee and Marietta Downes, John Fredericks, Joe and Joanne Lang, Bill McSeverny, Mike and Karen Eddy, Deb and Dan Kauffman, AnnaMarie and Howard Harrod, Karen Feather, John Noyes, the Hohnburger family, the Chrismans, the Hoilands, the Ostrums, the Pittmans, the Sullivans, the Wernicks, Elmer Bensen, Bud and Eunice James, and Chrys Landrigan. Lee Secrest deserves special thanks for assistance on the project but more critically, for enhancing the social life for all on the project. We appreciate the homes graciously provided to us by Ray Hart and Stuart McPherson. We very much miss the incredible place of the North Fork and hope to visit it often.

We also appreciate the cooperation of the wild members of the North Fork community for allowing us to intrude into their homes. The patience of grizzly bears, particularly near carcasses, is especially appreciated. We hope that our research efforts will enhance the understanding, appreciation, and respect for this incredible community and place.

Dave Hoerner of Eagle Aviation served as an exceptional pilot and provided countless hours of safe and humor-filled flights.

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Finally, I thank Wendy Clark, my partner and companion in all of this. Wendy was an excellent field assistant both when she was employed by the project and when she wasn't.

She volunteered a huge amount of her time and gave much of herself to me and this effort. Without her refined touch, my techs probably would have revolted on numerous occasions. Wendy is the best technical editor I know, and project reports, correspondence, and this dissertation have benefitted enormously from her skills. This project has been in most ways as much hers as mine. Wendy sacrificed much so that I could pursue this project, but I know she agrees with me that the opportunity to live 4 years in the North Fork easily made it worth the costs. Wendy made everything that was wonderful about life in the North Fork even more wonderful. We did it, thank you.

And lastly, to the memory of Burney Dunn, a former technician, a promising biologist, and good friend too soon lost. We very much wish Burney was still here to see he was right; persistence did result in a PhD dissertation.

CHAPTER 1: OVERLAP IN PREY KILLED BY WOLVES, COUGARS, AND HUMANS IN AND NEAR GLACIER NATIONAL PARK, MONTANA

Abstract: We compared patterns of prey selection among wolves (Canis lupus), cougars (Puma concolor), and humans to ascertain the effects of wolf recolonization and multiple predators on prey and on each other. Characteristics of prey selected by wolves and cougars in the same ecosystem have not been previously reported. White-tailed deer (Odocoileus virginianus) made up the greatest proportion of both wolf (0.83) and cougar diets (0.87), but elk (Cervus elaphus) and moose (Alces alces) made up a larger proportion of wolf (0.14, 0.03, respectively) than cougar (0.06, 0.02, respectively) diets. Wolves and cougars selected the same age classes in both deer and elk. They both selected older and younger deer and elk than hunters did. They both selected fewer males than hunters did and they both selected more fawns and more males than expected based on availability. Cougars killed relatively more bull elk than wolves. Cougars generally killed animals in poorer condition than wolves did, especially in elk. These data may be used by predator/prey managers to anticipate effects of wolf and cougar presence on populations of prey and may also be used to determine potential impacts of one predator on the other. We suggest possible management alternatives to mitigate effects.

INTRODUCTION

Wolves and cougars are the 2 carnivores at the top of the terrestrial food chain in North America. These predators were widespread and their ranges overlapped extensively prior to European settlement of the continent. Prior to 1995, wolves and cougars were sympatric only in Greater Glacier National Park in the United States. They both now occur in central Idaho and Greater Yellowstone following the reintroduction of wolves in early 1995.

These 2 predators greatly influenced the communities they inhabited, especially their cervid prey base (Bergerud 1988, Berger and Wehausen 1991, Hatter and Janz 1994, McNay and Voller 1995, Boertje et al 1996, Wehausen 1996), and together might be considered keystone predators (Mills et al. 1993, McLaren and Peterson 1994). Other than the work we report here, no study has simultaneously examined wolves, cougars, and their cervid prey.

Selection of prey is of primary interest in the ecology and management of these predators and their prey. Wolves and cougars generally employ 2 different hunting techniques. Wolves hunt in packs and are generally considered to be a coursing predator relying on speed over relatively long distances (Mech 1970). Cougars are a solitary stalking predator relying on surprise and short pursuits (Hornocker 1970). As a result of these contrasting techniques, differences in characteristics of prey selected (species, age, sex, and condition) by these 2 carnivores have been hypothesized (Schaller 1972, Kruuk 1972).

Additionally, it is probably more difficult for prey to escape predation when they live with predators that employ different hunting strategies (Kotler et al. 1992). Alternately, wolves and cougars may interfere with one another and, as a result, the survival rate of their prey may increase (Taylor 1984).

Evidence from Africa for the coursing/stalking dichotomy is both sparse and contradictory (Kruuk 1972, Schaller 1972, Reich 1981, Fitzgibbon and Fanshawe 1989). Habitat and the species and behavior of prey may have as much influence as hunting technique on selection of prey by predators. Information on prey selection of sympatric wolves and cougars is currently unknown. Knowledge of this system and of the factors influencing it will aid in predicting the effects on prey populations and may offer possibilities for reducing the impacts of predation. Additionally, this information will provide an indication of what effects these predators will have on each other as the range of overlap of wolves and cougars continues to expand.

We examined predation by wolves and cougars in and near Glacier National Park from 1992 through 1996 to determine: species, sex, age, and condition of prey selected by each.

STUDY AREA

The study was conducted in the North Fork of the

Flathead River drainage in northwestern Montana and southeastern British Columbia (Fig. 1) from December 1992 through April 1996. The study area encompassed the range occupied by wolves in Glacier National Park (GNP), and extended from Camas Creek in GNP northward to approximately 30 km beyond the Canadian border. The Whitefish divide formed the western border of the study area and the Livingstone Range the eastern border. The valley bottom varied from 4-10 km in width and rose from 1,024 m elevation in the south to 1,375 m in the northern part of the study area. Land east of the North Fork of the Flathead River (south of Canada) lies in GNP. West of the river, land ownership was a mosaic of Flathead National Forest, Coal Creek State Forest, and private property. Only 4 people resided permanently in the British Columbia portion of the study area, and approximately 150 people resided in the Montana portion.

The climate of this area is transitional between a northern Pacific coastal type and a continental type. Mean monthly temperatures ranged from -9 C in January to 16 C in July (Singer 1979). Snow normally covered the area from mid-November through mid-April. Average maximum snow depth at the Polebridge Ranger Station was 65 cm. Dense forests of lodgepole pine (Pinus contorta) dominated most of the North Fork valley, but sub-alpine fir (Abies lasiocarpa), spruce (Picea spp.), western larch (Larix occidentalis), and

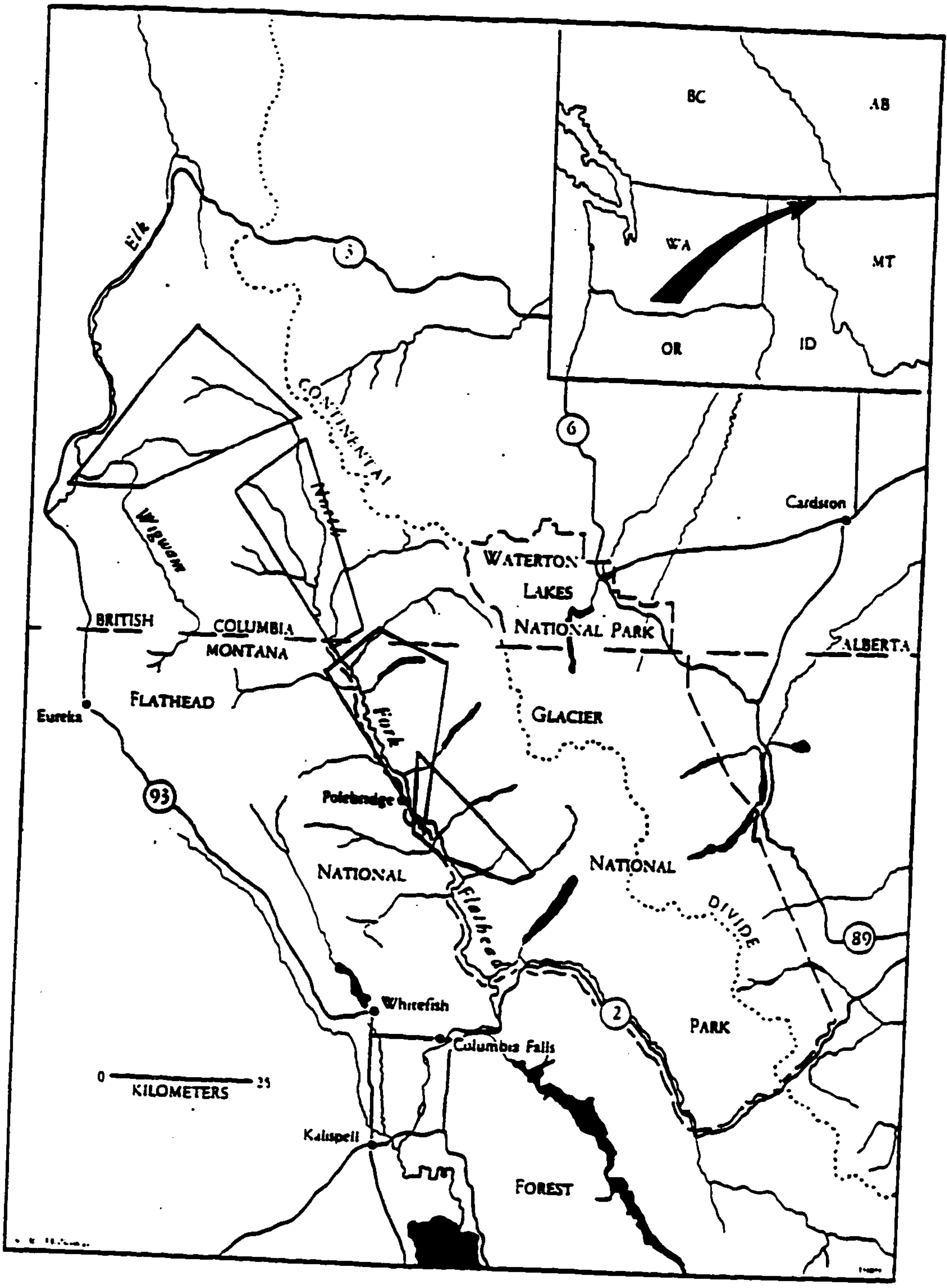

Figure 1. Map of study area and general distribution of wolf territories within the North Fork of Flathead River Basin, Montana and British Columbia.

Douglas-fir (Pseudotsuga menziesii) communities existed throughout the valley. Abundant meadows and riparian areas were dispersed throughout the study area. Detailed descriptions of vegetative communities in this area have been provided by Habeck (1970), Jenkins (1985), and Krahmer (1989).

Approximately 30-40 wolves in 3-4 packs occupied the study area (ca. 10 wolves/1000 km^2). The resident cougar population in the study area was estimated at 37-44 (ca. 10/1000 km^2, T.K. Ruth, Hornocker Wildl. Res. Inst., pers. commun). McLellan (1989) estimated the grizzly bear (Ursus arctos) density to be 63 bears/1000 km^2 for southeastern B.C. and he estimated the black bear (Ursus americanus) density to be 3 times greater than that.

METHODS

Wolves were captured, sedated, and radio-tagged (Mech 1974, Ream et al. 1991). Wolves were located from the ground or the air > 4 times per week during winter (Nov-Apr) so that we could locate their travel routes. We followed these travel routes on skis or snowshoes 1-2 days after wolves had left the area to locate kills made by wolves.

Cougars were captured using hounds released on cougar tracks (Murphy et al. 1992) and then immobilized and radio-tagged (Hornocker and Wiles 1972). Cougars living near roads were located daily from the ground, and all cougars were located weekly from the air. Kills made by cougars were located by snow-tracking radio-tagged cougars, by following cougar tracks during capture efforts, and occasionally while following travel routes of wolves.

White-tailed deer and elk were captured in traps (Clover 1956) and moose were captured by net-gunning or darting from a helicopter. Females were fitted with radio transmitters containing mortality sensors and were monitored 2-3 times per week. When a mortality signal was received, the collar was located and the site and any remains were examined to determine cause of death. Mortality signals were usually investigated 1-4 days after death. Predation was considered the cause of death when blood, subcutaneous hemorrhaging at wound sites, or sign of a struggle was found at the site. Predator hair, tracks, or scats, and carcass characteristics such as whether the carcass was buried, presence/absence of plucked hair, the kill and feeding pattern, and percent of carcass found was used to classify the predator responsible for death (O'Gara 1978). We used a key based on these characteristics and the work of others (Hatter 1984, Whitten et al. 1985) to categorize wolf and cougar kills as either certain, probable, or possible. Only kills categorized as certain or probable were used in the analysis.

Species of each carcass located while snow tracking was classified based upon size, hair pattern, and skeletal characteristics. Deer carcasses for which there were not enough remains to classify species were classed as white-tailed deer when they were discovered in white-tailed deer winter ranges. Sex of the carcass was determined by presence of antlers or pedicels, length of hind foot (Fuller et al. 1989) or pelvis characteristics (Edwards et al. 1982). An incisor, if present, was pulled to estimate age (Mattson's Lab., Milltown, Mont); otherwise, age was based upon tooth wear eruption and wear (Severinghaus 1949), skull size, or length of hind foot.

Femur marrow, when present, was collected from each carcass. These samples were double wrapped in plastic and kept frozen until they were weighed and then oven-dried at 60° C for 48 hours and reweighed. The dry weight of the marrow expressed as a percentage of its fresh weight was used to estimate percent fat (Neiland 1970). Marrows were also grouped into 4 classes based on appearance and texture (Neiland 1970). Diastema and hind foot length were also measured on each carcass when possible.

Species, sex, age, and month of death of kills were cross-tabulated by predator responsible. We used Pearson Chi-square analysis to test the null hypotheses of independence among categories. When > than 20% of cells had expected values < 5, we combined adjacent categories. Adjusted standardized residuals ([observed - expected/expected$^{0.5}$]/standard error) were computed to identify significant cells (Habermann 1973). Probability values used for determining significance were adjusted by dividing by the number of cell pairs in the cross-tabulation (Bonferroni adjustment-e.g. overall P < 0.10 and cell pairs = 5 , 0.10/5 = 0.02; Miller 1981:219).

Manly's (1974) alpha was calculated for each prey species using the constant prey population method to estimate selectivity of wolves and cougars:

$$\text{alpha} = \frac{r_i}{n_i} \cdot \frac{1}{\Sigma\ (r_j/n_j)}$$

where r_i, r_j = proportion of prey i or j in the diet (i and j = 1,2,..., m)

n_i, n_j = proportion of prey type i or j in the environment

m = number of prey species possible.

Alpha values are normalized such that $\Sigma\ \alpha = 1.0$. Thus, if predation is non-selective, $\alpha = 1/m$; a value > 1/m for a prey item indicates that it is selected.

Standard errors of the alpha values were also estimated following Manly (1974). Selectivity values were calculated using systematic transects as an estimate of available prey. Systematic transects followed hiking trails and roads throughout the study area (Fig. 2). Relative densities of prey were estimated at 1 km intervals along these transects by skiing 2

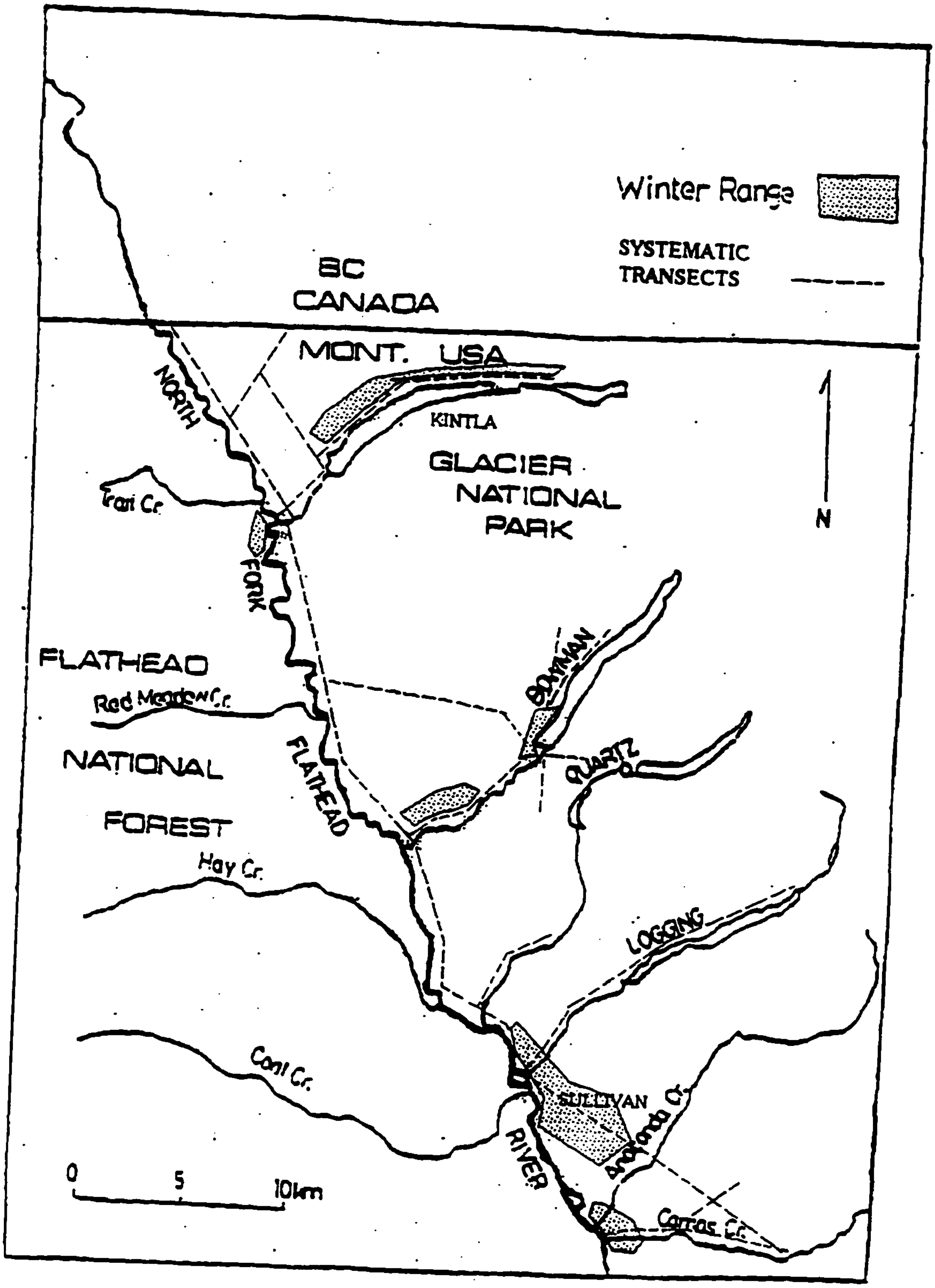

Figure 2. Distribution of systematic track transects and white-tailed winter ranges within Glacier National Park.

100 m transects in opposite directions perpendicular to the trail or road. If the transects were on an incline, they were oriented up and down the slope. The distance to the first white-tailed deer, elk, and moose track on each transect was recorded. The number of deer, elk, and moose tracks located on both transects (0, 1, or 2; only the first track was recorded) was divided by the distance to that track (e.g. 1/190 if one deer track was found at 90 m in one direction and no deer track was found along the opposite 100 m transect) to obtain the number of deer, elk, and moose tracks/m. This value was divided by the number of days since the most recent snowfall of > 5 cm to adjust for snowfall effects. Seven was the maximum number of days elapsed since snowfall because we assumed that after this track deposition had plateaued and tracks started to deteriorate (K. Kunkel, pers. obs.).

Ages and femur marrow fat of prey killed were not normally distributed so medians were compared using Kruskall-Wallis and Mann-Whitney U tests. Statistical differences between means of hind foot and diastema lengths of prey killed by wolves, cougars, and hunters were determined by ANCOVA using age of prey (months alive) as the covariate.

We operated the North Fork hunter big game check station each year to estimate the age and sex composition of hunter-killed deer and elk. We also measured the diastema of each animal coming through the station. Hunters could harvest bucks and bull elk throughout the 5-week hunting season. Does could be harvested the first 8-15 days of the season (depending on the yr) and cow elk could only be harvested the first 8 days. Beginning in 1994, cow elk could only be taken by permit and 20 permits were issued.

We conducted roadside counts of deer in open fields on approximately 10 evenings in late April and early May each year to estimate short yearling/doe ratios and to classify deer by sex. We drove a 13 km transect beginning one hour before sunset and counted and classified deer through a spotting scope.

Elk were counted and classified by sex and age in helicopter surveys that were flown in April or May 1993-96. For this survey, the study area was stratified into subunits (19 low, 5 medium, and 5 high density subunits) as outlined by Unsworth et al. (1994). All elk visible to the pilot and 2 observers were counted and classified by sex and age in a sample of these subunits each year. Population estimates were computed via a sightability model (computer program AERIAL SURVEY [Unsworth et al. 1994]).

Multiresponse permutation procedures (MRPP), a nonparametric statistical test (Mielke et al. 1976), was used to compare distributions of locations of wolf kill sites to locations of cougar kill sites and to compare locations of cougar kill sites found by snow tracking wolves to locations of cougar kill sites found by snow tracking cougars. Multiresponse permutation procedures compare the intragroup average distances with the average distances that would have resulted from all the other possible combinations of the data under the null hypothesis of no difference in distributions. The MRPP does not require normality or equal variances between groups (Zimmerman et al. 1985). The *P* values (calculated using program BLOSSOM [Slauson et al. 1994]) indicate the probability that the distribution of wolf kills and cougar kills were the same.

RESULTS

We followed 30 radio-tagged wolves in 3-4 packs from May 1992 through April 1996. Aerial counts made in May of each year indicated packs consisted of 5, 11, 3, and 4 wolves in 1992; 10, 7, 5, and 6 in 1993; 11, 3, and 7 in 1994; 10, 4, and 10 in 1995; and 12, 5, and 6 in 1996. Most of the carcasses we located were remains of kills made by wolves in the South Camas and North Camas packs south of the Canadian border (Fig. 1). We followed 40 radio-tagged cougars from December 1992 through April 1996. We monitored mortality in 64 radio-tagged female white-tailed deer, 53 elk, and 46 moose from 1990 through 1996.

We found 149 wolf-killed white-tailed deer, 34 wolf-killed elk, 134 cougar-killed white-tailed deer and 25 cougar-killed elk from 1992-1996 (Table 1). The number of

Table 1. Methods for locating white-tailed deer and elk killed by wolves and cougars in and near Glacier National Park, 1992-1995.

	white-tailed deer				elk			
	wolf-killed		cougar-killed		wolf-killed		cougar-killed	
Method	n	%	n	%	n	%	n	%
snow-tracking wolves	62	(42)	16	(12)	14	(41)	1	(4)
snow tracking cougar	10	(7)	55	(41)	1	(3)	2	(8)
aerial/misc	67	(45)	49	(37)	16	(47)	10	(40)
radio-tagged	10	(7)	14	(10)	3	(9)	12	(48)
Total	149		134		34		25	

elk kills located from 1992-1996 was too small to analyze so we augmented the sample with an additional 68 wolf kills and 8 cougar kills found from 1984-1991. We found 23 wolf-killed and 2 cougar-killed moose and 1 wolf-killed and 7 cougar-killed mule deer (Odocoileus hemionus). Moose and mule deer samples were too small for analysis. Hunters brought 270 white-tailed deer and 204 elk through the check station during the 1991-95 hunting seasons.

The spatial distribution of cougar kills resulting from located kills by backtracking wolves versus backtracking cougars was not different ($\underline{P} = 0.12$). Similarly, there was no difference in the spatial distribution of wolf kills versus cougar kills ($\underline{P} = 0.35$).

Timing of wolf versus cougar kills did not differ by months over the course of winter (Table 2) for either white-tailed deer ($\chi^2 = 1.53$, 3 df, $\underline{P} = 0.67$) or elk ($\chi^2 = 2.72$, 2 df, $\underline{P} = 0.26$).

The relative proportion of deer, elk, and moose in wolf and cougar diets differed ($\chi^2 = 6.10$, 2 df, $\underline{P} = 0.048$; Table 3). Elk made up a marginally greater proportion of wolf diets (0.14) than cougar diets (0.06; $\underline{Z} = 2.20$, $\underline{P} = 0.08$).

Deer tracks were 4.6 times more frequent than elk tracks and 7.8 times more frequent than moose tracks encountered on systematic transects (Table 3). Cougars selected deer (Manly's alpha = 0.39 ± 0.01) over elk (0.12 ± 0.03) and moose (0.17 ± 0.15) when compared to availability

Table 2. Timing of wolf and cougar kills made during winters 1992-1996 in and near Glacier National Park.

	Wolf kills		Cougar kills	
Month	n	%	n	%
Dec	12	(9)	7	(6)
Jan	42	(30)	41	(37)
Feb	58	(42)	43	(38)
March	25	(18)	18	(16)
April	2	(1)	3	(3)
Total	139		112	

Table 3. Species of prey selected by wolves and cougars in and near Glacier National Park, 1992-96.

	Wolf		Cougar		Systematic	
Species	Prop.	n	Prop.	n	Prop.	tracks /km
White-tailed deer	0.826	(138)	0.874	(118)	0.744	(14.8)
Elk	0.137	(23)	0.059	(8)	0.161	(3.2)
Moose	0.029	(5)	0.015	(2)	0.096	(1.9)
Mule deer	0.005	(1)	0.052	(7)		

along systematic transects. Wolves selected deer (0.37 ± 0.01) over elk (0.29 ± 0.02), while moose were selected as available (0.34 ± 0.19).

Year-round, cougars killed more radio-tagged elk (12) than did wolves (3), but the relative proportions of radio-tagged white-tailed deer and elk in cougar and wolf diets did not differ (14, 12 vs. 10, 3, respectively; $\chi^2 = 1.95$, 1 df, $P = 0.163$).

Age

Deer

The median age of male deer killed by wolves (3.5, $n = 34$), cougars (2.0, $n = 46$), and hunters (2.5, $n = 188$) did not differ (Kruskall-Wallis $\chi^2 = 0.296$, 2 df, $P = 0.862$). However, the age distribution among the 3 groups did differ ($\chi^2 = 89.65$, 6 df, $P < 0.0001$; Table 4). The age distribution of wolf kills versus hunter kills was different ($\chi^2 = 23.22$, 3 df, $P < 0.001$). Wolves killed more male fawns ($Z = 4.0$, $P = 0.0002$) and ≥ 6.5 yr olds ($P = 0.0008$) and less 1.5-2.5 yr olds ($P = 0.002$) than did hunters. The age distribution of cougar kills versus hunter kills was also different ($\chi^2 = 63.13$, 3 df, $P < 0.001$). Cougar killed more fawns ($P < 0.00001$) and ≥ 6.5 yr olds ($P = 0.0006$) and less 1.5-2.5 yr olds ($P = 0.0002$) than did hunters.

The median age of female deer killed by hunters (2.5, $n = 83$), cougar (2.5, n= 44), and wolves (5.0, $n = 36$) was

Table 4. Ages of non-radioed white-tailed deer killed by wolves, cougars, and hunters in and near Glacier National Park, Montana from 1992-96[•].

	Wolf-killed			Cougar-killed			Hunter-killed		
Age	M	F	Total	M	F	Total	M	F	Total
< 1	8a(24)	8 (22)	16	16b(35)	16 (36)	32	8ab(4)	13 (16)	21
1-2	8a(24)	7a(19)	15	9b(20)	9b(21)	18	98ab(52)	35ab(42)	133
3-5	11 (32)	6 (17)	17	12 (26)	8 (18)	20	75 (40)	30 (36)	105
6-7	4a(12)	4a(11)	8	5b(11)	3b(7)	8	3ab(2)	5 (6)	8
8-9	2 (6)	2 (6)	4	4 (9)	5 (11)	9	2 (1)	0 (0)	2
10+	1 (3)	9 (25)	10	0 (0)	3 (7)	3	2 (1)	0 (0)	2
Total	34 (49)c	36 (51)		46d(51)	44 (49)		187cd(69)	83 (31)	

[•] within each table row, value sharing similar letters differ as follows:

a $\underline{P} < 0.025$ (0.10/4 pairs)
b $\underline{P} < 0.025$
c $\underline{P} < 0.05$
d $\underline{P} < 0.05$

different (Kruskall-Wallis $\chi^2 = 11.36$, 2 df, $P = 0.0031$). The median age of female deer killed by wolves was greater than the median age of female deer killed by cougars (Mann-Whitney $U = 600.5$, $Z = -1.88$, $P = 0.0598$) and hunters (Mann-Whitney $U = 1016$, $Z = -2.79$, $P = 0.0052$). The age distribution of female deer killed by wolves, cougars, and hunters was also different ($\chi^2 = 35.01$, 6 df, $P < 0.0001$). There was no difference between wolves and cougars ($\chi^2 = 3.31$, 4 df, $P = 0.507$) but hunters differed from both wolves and cougars ($\chi^2 = 34.23$, 4 df, $P < 0.001$; $\chi^2 = 23.79$, 4 df, $P < 0.001$, respectively). Wolves and cougars killed more $\geq$ 6.5 yr old female deer ($P < 0.00001$; $P = 0.002$, respectively) and less 1.5-2.5 yr old deer ($P = 0.016$, $P = 0.016$, respectively) than did hunters. Cougars also killed more fawns ($P = 0.009$) than did hunters.

The median age of female deer killed by wolves (5.0) was significantly greater than that of males killed by wolves (3.5; Mann-Whitney $U = 463.0$, $Z = -1.77$, $P = 0.0774$, $n = 70$). There was no difference in the median age of male and female deer killed by cougars (2.0 vs 2.5; Mann Whitney $U = 992.0$, $Z = -0.166$, $P = 0.869$, $n = 90$).

The median age of radio-tagged deer killed by cougars (6.5, $n = 12$) was greater than the median capture age (4.5, $n = 58$; Mann-Whitney $U = 211.5$, $P = 0.0322$). There was no difference between median age of wolf kills (4.5, $n = 9$) and capture age (4.5; Mann-Whitney $U = 240.0$, $Z = -0.3890$, $P =$

0.697) or between median ages of wolf and cougar kills (4.5 vs 6.5; Mann-Whitney $\underline{U} = 31.5$, $\underline{P} = 0.108$).

When sexes were combined (1990-96), wolves and cougars killed more fawns (0.32, 0.36, respectively) than did hunters (0.06; $\chi^2 = 69.9$, 1 df, $\underline{P} < 0.001$; $\chi^2 = 70.21$, 1 df, $\underline{P} < 0.001$, respectively) and a greater proportion of fawns than expected based on availability based on roadside counts (0.19, $\underline{n} = 96$; $\chi^2 = 11.81$, 1 df, $\underline{P} = 0.001$; $\chi^2 = 13.65$, 1 df, $\underline{P} < 0.0001$, respectively). Hunters killed a lower proportion of fawns than expected based on availability ($\chi^2 = 34.46$, 1 df, $\underline{P} < 0.0001$).

Elk

There was no difference in the age distribution of elk (sexes combined, 1984-96) killed by wolves versus cougars ($\chi^2 = 5.41$, 3 df, $\underline{P} = 0.144$; Table 5). The age distribution of elk killed by wolves and cougars was different from hunters ($\chi^2 = 34.51$, 3 df, $\underline{P} < 0.0001$; $\chi^2 = 27.35$, 3 df, $\underline{P} < 0.0001$, respectively). Wolves and cougars killed more calves ($\underline{P} < 0.00001$; $\underline{P} = 0.012$, respectively) and > 9 yr old elk ($\underline{P} = 0.016$; $\underline{P} < 0.00001$, respectively) and less 1-3 yr old elk than hunters ($\underline{P} = 0.012$; $\underline{P} = 0.004$, respectively). Wolves killed less 4-9 yr old elk than hunters ($\underline{P} = 0.0026$). Wolves and cougars killed proportionately more calves than expected based on aerial surveys ($\chi^2 = 51.68$, 1 df, $\underline{P} < 0.0001$; $\chi^2 = 8.16$, 1 df, $\underline{P} = 0.004$, respectively; Table 5).

The median age of radio-tagged elk killed by cougars

Table 5. Age and sex of elk killed by wolves, cougars, and hunters and from helicopter counts (elk classed as calves or adults; 1993-1996) in and near Glacier National Park, 1986-96[*].

Age/ sex	Wolf-killed n	Prop.	Cougar-killed n	Prop.	Hunter-killed n	Prop	Aerial n	Prop.
< 1	35ac	(0.36)	7bd	(0.29)	17ab	(0.11)	116cd	(0.11)
1-3	35a	(0.36)	5b	(0.21)	83ab	(0.52)	971	(0.89)
4-9	15a	(0.15)	5	(0.21)	52a	(0.33)		
> 9	12a	(0.12)	7b	(0.29)	7ab	(0.04)		
M	35eg	(0.48)	17efg	(0.77)	113fg	(0.55)	147g	(0.15)
F	38	(0.52)	5	(0.23)	91	(0.45)	824	(0.85)

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[*] within each table row, value sharing similar letters differ as follows:

a $P < 0.025$ (0.10/4 pairs)
b $P < 0.025$
c $P < 0.05$
d $P < 0.05$
e $P < 0.05$
f $P < 0.05$
g $P < 0.05$

(10.3, $\underline{n} = 12$) was greater than the median capture age (6.5, $\underline{n} = 55$; Mann-Whitney $\underline{U} = 210.0$, $\underline{Z} = -1.97$, $\underline{P} = 0.05$).

Sex

Deer

There was no difference in the sex ratio of deer killed by wolves (0.46 M; Table 4) versus cougars (0.49 M; $\chi^2 = 0.10$, 1 df, $\underline{P} = 0.748$). Wolves and cougars killed fewer males than did hunters (0.70 M; $\chi^2 = 17.89$, 1 df, $\underline{P} < 0.001$; $\chi^2 = 15.62$, 1 df, $\underline{P} < 0.001$, respectively). The sex ratio difference is significant only in the 1.5-2.5 yr old age group for cougars versus hunters ($\chi^2 = 4.21$, 1 df, $\underline{P} = 0.041$).

Wolves, cougars, and hunters killed proportionably more males than expected based on roadside counts (0.18 M, $\underline{n} = 397$; $\chi^2 = 52.03$, 1 df, $\underline{P} < 0.0001$; $\chi^2 = 28.12$, 1 df, $\underline{P} < 0.0001$; $\chi^2 = 293.48$, 1 df, $\underline{P} < 0.0001$, respectively).

Elk

Cougars killed a greater proportion of male elk than did wolves (0.74, $\underline{n} = 17$ vs 0.48, $\underline{n} = 35$; $\chi^2 = 4.75$, 1 df, $\underline{P} = 0.030$) and hunters (0.55, $n = 113$; $\chi^2 = 2.90$, 1 df, $\underline{P} = 0.089$). There was no difference in the sex ratio of wolf and hunter kills ($\chi^2 = 1.2$, 1 df, $\underline{P} = 0.274$). Based on helicopter counts, wolves and hunters killed proportionably more males > 1 yr old (0.50, $\underline{n} = 18$ and 0.72, $\underline{n} = 32$, respectively) than expected ($\chi^2 = 72.41$, 1 df, $\underline{P} < 0.0001$, χ^2

= 150.16, 1 df, $P < 0.0001$; Table 5). The sample size of cougar kills was too small to compare.

Nutritional Condition Index Comparisons

Male deer killed by cougars had shorter diastema lengths ($\bar{x} = 67.7$, SE = 2.5, $n = 13$) than did male deer killed by wolves ($\bar{x} = 71.4$, SE = 2.3, $n = 21$; $F = 12.0$; 1, 32 df; $P = 0.002$; Table 6) and hunters ($\bar{x} = 73.5$, SE = 0.59, $n = 157$; $F = 7.46$; 1, 168 df; $P = 0.007$). There was no difference in the length of wolf-killed and hunter-killed diastemas ($F = 1.80$; 1, 175 df; $P = 0.182$). There was no difference in diastema lengths of female deer killed by wolves, cougars, or hunters ($F = 1.8$; 1, 35 df; $P = 0.189$). Diastemas of male deer killed by wolves from 1984-96 ($\bar{x} = 75.8$, SE = 1.50, N = 40) were longer than diastemas from deer killed by hunters ($\bar{x} = 72.6$, SE = 0.35; $F = 4.15$; 1, 443 df; $P = 0.042$).

There was no difference between the hind foot lengths in wolf-killed or cougar-killed male deer nor was there any difference between hind foot lengths of female deer killed by the 2 predators (Table 6).

Femur marrow fat (FMF) ANCOVA using month of death as covariate indicated no effect of month ($F = 0.130$; 1, 126 df; $P = 0.719$). Because of this and because there was no difference in the timing of wolf and cougar kills, month of death was not used as a covariate in comparing (FMF) values

Table 6. Condition parameters of white-tailed deer killed by wolves, cougars and humans in and near Glacier National Park*.

	Wolf-killed						Cougar-killed						Hunter-killed					
	Males			Females			Males			Females			Males			Females		
Parameter	%	SD	n	%	SD	n	%	SD	n	%	SD	n	%	SD	n	%	SD	n
Femur Marrow Fat																		
86-96	82a	25	65	83	21	55	73b	31	33	84	26	30						
92-96	63	32	28	82	25	30	73	31	32	85	25	27						
94-96	89	15	11	86	27	5	80b	26	15	88	20	18						
Diastema Length (mm)																		
92-96	71.4d		21	69.9		16	67.7e		13	70.3		22	73.5f		157	66.6		81
	2.3g			1.7			2.5			1.8			0.6			0.9		
Hind Foot Length (mm)																		
92-96	49.0		14	46.0		8	45.4		10	47.1		16						
	4.2			1.2			1.0			0.6								

* letters following values in table indicate the following:

a medians reported for femur marrow fat

b Significant difference between wolf and cougar kill (P = 0.055)

c Significant difference between wolf and cougar kills (P = 0.0312)

d means reported for diastema and hind foot length

e Siginificant difference between wolf and cougar kills (P = 0.002)

f Significant difference between cougar and human kills (P = 0.007)

g standard error of means reported for diastemas and hind foot lengths of wolf and cougar kills.

There was no difference in the FMF of male or female deer killed by wolves versus cougars ($\underline{P} = 0.880$; $\underline{P} = 0.414$, respectively; Table 6). When the winter of 92-93 (most severe winter) was excluded, FMF of female and male deer killed by cougars was lower than the FMF of wolf kills ($\underline{P} = 0.06$; $\underline{P} = 0.0312$).

Marrow class distribution (sexes combined, 1992-96) differed between wolves and cougars ($\chi^2 = 12.08$, 6 df, $\underline{P} = 0.062$). A greater proportion of wolf kills than cougar kills were in the class 4 (best condition) category ($\underline{P} = 0.021$).

Elk killed by cougars (including possible wolf and cougar kills; 1986-96; sexes combined) had lower FMF values (med = 0.63, SD = 0.194, $\underline{n} = 16$) than elk killed by wolves (med = 0.77, SD = 0.188, n = 60, $\underline{P} = 0.057$; Table 6). Sample sizes were too small for hind foot length and diastema comparisons in elk.

From 1986-96, cougars visited or scavenged 11 (2.9%) of 381 wolf kills while wolves visited or scavenged 33 (20.1%) of 164 cougar kills.

DISCUSSION

Species of prey selected by wolves varies greatly among regions due to varying availability of prey. Based on the examination of 9 studies where wolves lived among high ungulate diversity, Weaver (1994) concluded that wolves specialize on elk and moose, but readily generalize to deer ("expanding generalists"). In our study area, wolves selected for encounters with deer over elk (hunted deer winter ranges; chapter 4), but within these winter ranges selected elk over deer. Wolves killed moose in proportion to their availability.

The diets of cougars are generally very broad, and hemisphere-wide, cougars are probably "one of the most adaptable and generalist mammalian carnivores" (Iriarte et al. 1990: 188). However, in most regions of temperate North America they specialize on deer. In 14 of 16 studies reviewed by Anderson (1983), deer was the major food item in cougar diets. The size and solitary behavior of cougars limits them to moderate-sized cervids (Sunquist and Sunquist 1989). This probably explains why, during winter, wolves killed a greater proportion of elk and moose than cougars. Reports of cougars killing adult moose are very rare, although calves were an important part of cougar diets in Alberta (Ross and Jalkotsky 1996). Elk did make up the greatest proportion of the diet of cougars in the northern Yellowstone Ecosystem (4 times more elk killed than mule deer; Murphy et al. 1992), but based on availability (elk 10 times more abundant than mule deer; Singer 1990), deer may have been selected over elk. Based upon the estimates of elk and mule deer populations made by Hornocker (1970), cougars may have selected elk over mule deer in central

Idaho. Deer comprised 40% of the diet of cougars in Alberta while moose and elk comprised 23% and 15%, respectively (Ross and Jalkotzky 1990). No estimates of availability were reported in the Alberta study. Cougars also killed a greater percentage of deer (41%) than elk (27%) along the Rocky Mountain Front in Montana (Williams et al. 1995). No estimates of availability were reported here either.

At least in the relatively early stages of wolf recolonization in Greater Glacier, competition between wolves and cougars has not resulted in significant partitioning of prey species between these 2 predators. A partial explanation for this may be the large amount of prey biomass available at the initiation of wolf recolonization. Gross estimates place the ungulate biomass index per wolf (Fuller 1989) in our study area among the highest measured in North America (250:1; K. Kunkel, unpubl. data). This does not necessarily mean that over time, cougar prey selection will not change as a result of competition with wolves. Bobcat diets in Maine may have shifted 10 years after colonization by coyotes (Litvatis and Harrison 1989). Iriarti et al. (1990) speculated that prey selection by cougars is influenced by competition from larger jaguars. Cougars are generally smaller in areas where they are sympatric with jaguars (Iriarti et al. 1990).

Based on radio-tagged deer, elk, and moose, elk made up a greater proportion of cougar diets than they did of cougar diets estimated from snow tracking. This proportion was also greater than the proportion of elk in the winter diets of wolves. Nine of the 11 radio-tagged elk were killed by cougars from March-May. Elk may be particularly vulnerable to cougars as a result of poor condition following winter. Additionally, elk may be vulnerable as they migrate to summer range through habitats particularly amenable for stalking by cougars (chapter 3). Ten of the 11 radio-tagged elk were killed by cougars in 1990-1992 before the intensive snow tracking of cougars began. Since then, cougar-caused mortality rates on elk have significantly declined (chapter 2). This may have resulted from the declining elk population (chapter 2) or other factors including competition with wolves. Two potential biases in the way we located carcasses also may account for the differences between cougar diets estimated by snow tracking versus radio-tagging. First, we found more kills made by female than male cougars as a result of a greater number of female cougars captured (35 female years vs 9 male years). Characteristics of prey killed by females and males may differ. Ross and Jalkotzky (1996) reported that while females cougars killed mostly elk and mule deer, males specialized on moose. Our radio-tagged cougars may, however, represent the sex ratio of the population in which case there is no bias. Second, areas that we located carcasses in were the more accessible portions of the study area, and more mule deer may have been killed by cougars and wolves in more remote or rugged portions of the study area.

We found that, similar to many studies, wolves and cougars primarily kill individuals that are the most vulnerable in the population (for synthesis on wolves see Mech 1996). In several studies, cougars killed older individuals and males in greater proportions than available in the population (Robinette 1959, Hornocker 1970, Spalding and Lesowski 1971, Shaw 1977, Ackerman et al. 1984). Elk calves were the predominant prey item killed by cougars in the northern Yellowstone Ecosystem (Murphy et al. 1992). Alternately, O'Gara and Harris (1988) found cougars selecting deer in prime condition (based on age and femur fat consistency). The majority of these deer were males and might have been more conspicuous or in relatively poor condition due to rutting behavior although marrow consistency did not indicate the latter. O'Gara and Harris (1988) speculated that male mule deer in their prime used habitats that exposed them to greater cougar predation risks. We agree with Mech (1996) that some traits predisposing prey to wolves are subtle and not easily measured and that the same is probably true for other carnivores.

We recognize that marrow fat values only provide an index of animal condition when an animal is already in relatively poor condition (Mech and DelGuidice 1985); for this reason, we used femur marrow fat (FMF) to compare condition of prey killed by wolves relative to cougars. While most of the marrow fat levels in animals we found were not low enough to result in death of the animal, they were indicative of animals of reduced vigor and vitality (Mech et al. 1995). Diastema also served as an indicator of relative condition. Diastema length responds rapidly to decreased food competition or improved range conditions (Reimers 1972). Frisina and Douglass (1989) found that diastema measurements corresponded to weight differences in male mule deer.

Based on age, sex, and condition parameters, wolves and cougars killed very similar deer. A potential bias that may have affected this finding is that because wolves occasionally completely consume fawns, we might have under-reported the number of fawns killed by wolves. Discounting this, there was little indication of resource partitioning between these 2 predators. We found little support for the differences in prey selection that were hypothesized to result from the different hunting techniques used by the 2 predators. In fact, the predator assumed to rely less on physically compromised prey, cougars, selected a greater proportion of animals in poorer condition. This was especially true for the larger and potentially more dangerous prey, elk. Cougars selected more males and more elk with lower femur fat than did wolves. Males were assumed to be in poorer condition than females owing to the significant energy drain of male rutting activities (Clutton-Brock et al. 1982), but we do not rule out the possibility that other factors increased male vulnerability (Fitzgibbon 1990).

Wild dogs (*Lycaon pictus*) in the Serengeti killed a greater proportion of gazelles (*Gazella thomsoni*) in poor condition than cheetahs (*Acinonyx jubatus*) did, as predicted by the hunting dichotomy (Fitzgibbon and Fanshawe 1989). However, Fitzgibbon and Fanshawe (1989) speculated that this may have resulted from factors unrelated to condition. Wild dogs did not kill more young and old gazelles than cheetahs possibly because cheetahs were able to distinguish more vulnerable animals without chasing them. Prey exhibiting slower reaction times are no doubt more vulnerable to any type of predator. Geist (1978) documented that underdevelopment and poor nutrition is associated with increased time of neural processing. This may account for part of the apparent selection exhibited by cougars in our study. Cooperative hunting by wolves and relatively dense stalking cover may be part of the reason we found evidence in direct contrast to predictions of the hunting dichotomy.

Cooperative hunting may allow wolves to take less vulnerable prey than cougars which have to bring down large and dangerous prey on their own. Additionally, the rugged topography and thick vegetation of northwestern Montana probably results in relatively short chases by wolves, reducing the selection factor (Okarma 1984, Huggard 1993, K. Kunkel, unpubl. data). Under these circumstances (and probably others), wolves probably stalk their prey to close distances and then use a quick rush over a relatively short distance not too dissimilar from cougars (Mech 1970).

In multi-prey systems where elk are as abundant or more abundant than deer, greater resource partitioning between wolves and cougars may occur. Given equal encounter rates, wolves selected elk over deer. This is probably because, based on size, elk are more profitable prey (but see Huggard 1993). Cougars may have selected deer over elk because elk are at the upper limit size-class of prey that can be killed by cougars. This is born out by a greater percentage of less-fit elk than less-fit deer in the diet of cougars (Temple 1987). Alternately, Karanth and Sunquist (1995) reported that tigers (Panthera tigris) readily prey on gaur (Bos gaurus) which weigh 500-1000 kg and suggested that anti-predator behavior, rather than size, may be a more important defense against ambush predators. The more closed habitats preferred by deer over elk during winter in our study area (Jenkins and Wright 1988) probably makes the former more vulnerable than the latter to cougar predation (chapter 3). Wolf hunting success is influenced less by specific habitat features than is cougar hunting success (Mech 1970, Seidensticker et al. 1973, chapter 3). As a result, resource partitioning between wolves and cougars may also be more evident in landscapes with greater habitat heterogeneity than is present in our study area. Williams et al. (1995) speculated that vulnerability of mule deer, white-tailed deer, and elk to cougars on the Rocky Mountain Front varied due to differential habitat use among seasons by these species. We would anticipate that prey selection and predator dietary overlap will vary among landscapes (Christensen and Persson 1993).

Winter severity also probably plays a role in the amount of diet overlap between cougars and wolves. During more severe winters, deer are more concentrated in winter ranges (K. Kunkel, unpubl. data, Jenkins and Wright 1988, Fuller 1991) and this may result in greater wolf and cougar spatial overlap (T.K. Ruth, unpubl. data). Relative vulnerability of deer, elk, and moose changes with differences in winter severity and, as a result, prey selection may change (Mech et al. 1995, Dale et al. 1995). I found a significant relationship between percentage of deer in wolf diets and annual total winter depths in our study area (chapter 4).

Wolves visited cougar kills much more commonly than cougars visited wolf kills. We are uncertain of the biological importance of this phenomenon because we were unable to determine how much, if any, wolves consumed of these carcasses. Wolves are a more effective competitor than cougars at carcasses (T.K. Ruth, unpubl. data). We can only speculate what effect this might have on the prey base. If wolf consumption rates are significant, cougars may be forced to increase their kill rate. This was reported after scavenging by bears (Ursus spp.) on cougar kills in the Yellowstone area (K.M. Murphy, Hornocker Wildl. Inst, pers. commun.). Such a phenomenon may allow wolves to reduce their kill rate.

Niche relationships between species may be measured based on several parameters including activity patterns, space use, habitat use, and dietary overlap. For top-level predators like wolves and cougars, the most meaningful of these is dietary overlap. The primary activity of these animals is prey acquisition and prey is the limiting resource (Fuller 1989, but see Lindzey et al. 1994). Differences in temporal, spatial or habitat overlap are relatively less significant than diet (unless direct interspecific mortality is significant) because coexistence is ultimately determined by available prey for each species. For raptors, Jaksic (1982) found that major differences in the time of activity may not result in low dietary overlap, especially if the prey base is limited. As pointed out by Litvatis and Harrison (1989), a snowshoe hare (Lepus americanus) eaten at any hour influences the subsequent availability of hares. Similar logic holds true for spatial and habitat use, especially when prey consists of wideranging species like deer and elk. However, dietary overlap alone does not necessarily indicate the degree of competition (Lawlor 1980); but when combined with our observations of kleptoparasatism by wolves on cougar kills, direct killing of cougars by wolves (T.K. Ruth, unpubl. data, Boyd and Neale 1992), and apparent predator-related decline in the deer population (chapter 2), a reasonable argument for both exploitative and interference competition between cougars and wolves can be made. At this point, it seems unlikely that competition has resulted in a decline in the cougar population. Only 2 radio-tagged cougars have been killed by wolves. Cougars can readily escape wolf predation by climbing trees (T.K. Ruth unpubl. data, Cypher 1993). Six radio-tagged cougars have, however, died of starvation (T.K. Ruth, unpubl. data). The role of competition in this is unknown. Creel and Creel (1996) reported that wild dogs fare poorly where the percentage of dog kills fed on by hyenas (Crocuta crocuta) exceeded 60%. They also suggested that the highly overlapping diets of dogs and hyenas and resulting resource exploitation competition explained the negative correlation between densities of dogs and hyenas. Based on distribution of kills, we observed no evidence of this in wolves and cougars. More long-term research is needed on interactions between wolves and cougars to examine these possibilities.

MANAGEMENT IMPLICATIONS

Wolves and cougars will become sympatric throughout the western U.S. as wolf populations continue to expand. Based on our study, wildlife managers can expect competition for prey between these predators, especially in those ecosystems dominated by deer. When coupled with hunting pressure, lower deer equilibriums should be anticipated in these systems. The low elk:deer ratio in our study area may result in deer being maintained by intense cougar and wolf predation at lower equilibrium levels than in systems with higher elk populations (chapter 4). Alternate prey populations (elk and moose) might be enhanced to move some wolf predation pressure off deer. During more severe winters spatial overlap of deer and elk is greater (Jenkins and Wright 1988). Because wolves prefer elk over deer upon encounter, increased predation pressure on elk may occur during more severe winters. We found that while deer and elk older than 5 become more vulnerable to cougars and wolves, they were much less vulnerable than younger deer and elk to hunters. This suggests that there may be some potential to reduce hunter-caused mortality by managing for older age structures in deer and elk. Such a strategy also has value for increasing fawn and calf survival (Kunkel and Mech 1994, Ozoga and Verme 1986) which is very low in our study area.

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CHAPTER 2: MORTALITY AND POPULATION TRENDS OF CERVIDS IN A MULTI-PREY SYSTEM IN NORTHWESTERN MONTANA

Abstract: We examined mortality rates and population trends of white-tailed deer (Odocoileus virginianus), elk (Cervus elaphus), and moose (Alces alces) in an ecosystem where wolves (Canis lupus), cougars, (Puma concolor) bears (Ursus spp.), coyotes (Canis latrans), and humans were potential predators. The effects of such a suite of predators on prey has not been previously reported. Annual survival rates were 0.74, 0.83, and 0.88 for deer, elk, and moose, respectively. Cougars and wolves were the most significant source of mortality for deer and elk and wolves and bears were the most significant source of mortality for moose. Deer were vulnerable to predation throughout most of the year while elk and moose were primarily vulnerable during the fall and in early spring. All age classes of deer were vulnerable to predators while young and old moose and elk were most vulnerable. Moose survival rates were higher where wolves were absent and where white-tailed deer were present. Deer and elk population declines were positively correlated with wolf numbers. The moose population remained mostly stable, possibly resulting from the predator dilution effect provided by more vulnerable white-tailed deer. Predation appeared to be the major factor limiting deer and elk populations in this system. Predator/prey managers may

be able to manipulate cougar and alternate prey densities to enhance prey populations that are impacted by wolves, cougars, and bears.

INTRODUCTION

Recent emphasis in ecology and conservation biology has shifted from single-species management to multi-species and ecosystem management. Even so, few studies of large mammals in North America have concurrently examined species relationships in an ecosystem context. We initiated a study in 1990 to examine predator-prey relationships in a complex predator-prey ecosystem in northwestern Montana.

Most detailed predator-prey studies in North America have been conducted where only 1 or 2 main prey species and 1 or 2 large carnivores are present (Mech 1966, Pimlott et al. 1969, Hornocker 1970, Peterson 1977, Fritts and Mech 1981, Nelson and Mech 1981, Peterson et al. 1984, Ballard et al. 1987). Few studies have investigated predation in areas of high diversity of large predators and prey (Huggard 1993, Boyd et al. 1994, Weaver 1994). These studies, however, have focused on the predator side of the relationship and then have focused on only one predator. Little work has been done to simultaneously and directly examine prey or examine how prey cope with more than 1 predator. Data on the relative vulnerability of northern ungulates is very limited. Messier (1995) lamented this paucity of data because vulnerability of prey can drastically influence the shape of the functional response of predators, the knowledge of which is key to understanding the effects of predation on prey populations.

After a 50 year absence, wolves began recolonizing northwestern Montana in the mid 1980s (Ream et al. 1989). Since their recolonization and subsequent reintroduction into Yellowstone National Park in 1995, these have been the only 2 areas in the U.S. where the 3 top-level North American predators, wolves, cougars , and grizzly bears (Ursus arctos), have coexisted and it is therefore the only area where their combined effects on prey can be measured. The potential for such an assemblage to impact prey populations is substantial (Messier 1994). The effects of predators on prey populations has been one of the greatest concerns of the public about wolf recovery (U.S. Fish and Wildl. Serv. 1994). The Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildl. Serv. 1987) advocated the examination of the effects of wolf recovery on native ungulate populations as a top priority during recovery.

Wolf recovery will complicate management of prey populations. With the addition of another significant source of mortality and without adequate data on survival and cause-specific mortality, overexploitation becomes a possibility in intensively hunted prey populations (Boertje et al. 1996). Data on large mammal predator-prey relationships and particularly cause-specific mortality rates reduces the likelihood of such an occurrence.

Predator/prey relationships between large carnivores, white-tailed deer, elk, and moose were examined in the North Fork of the Flathead Valley in Montana from 1990 through 1996. Our overall objectives were to determine: (i) the causes, extent, and timing of mortality in adult female white-tailed deer (deer), elk, and moose; (ii) population trends of deer, elk, and moose; and (iii) the role of predators in these parameters. More specifically, we examined factors affecting the relative vulnerability of deer, elk, and moose to specific predators. We examined monthly, annual, snow-related, age-related, and condition-related factors affecting survival. We also examined the effects of wolf presence or absence and deer presence or absence on the relative survival rates of deer, elk, and moose. Finally, we examined the role of environmental and condition parameters in prey to assess the role of these factors relative to the role of predators in affecting population trends of deer, elk, and moose.

If deer, elk, or moose populations in the study area were declining, then: 1a) recruitment should not fully replace mortality and 1b) population indices including mean number of pellet groups, aerial counts, and hunter success should decline.

If predation was the primary factor limiting populations of cervids, then: 2a) predators should be the primary cause of mortality in cervids, 2b) predators should impact more than just the oldest and youngest age classes in cervids, 2c) cervid survival rates should be higher in portions of the study area where predator density is lower, 2d) predation rates should be additive, 2e) predator density should explain more of the variation in cervid population trends than snow depth or animal condition, and 2f) condition of cervids should be improving and hunter success should be decreasing more in our study area relative to other areas in the region with lower densities of predators.

METHODS

Survival Rates (predictions 1a and 2a)

Cervid trapping and mortalities

We captured white-tailed deer in traps (Clover 1956) on 3 winter ranges in GNP (Kintla Lake, Bowman Lake, and Logging Creek; Fig. 2, chpt. 1) during winter from 1990 through 1995. We captured elk in collapsible traps (Clover 1956) in the Big Prairie grassland in GNP during early winter and along the North Fork of the Flathead river bottom during mid-winter from 1990 through 1995. Moose were captured using darts filled with 3.9 mg Carfentanil (Meuleman et al. 1984) and 0.25 mg Rompun fired from a helicopter in January and December 1990. Carfentanil was reversed with 6 cc of Naloxone. Moose were net-gunned from a helicopter in December 1993. We fitted females of all 3 species with radio transmitters containing mortality sensors and pulled a tooth for aging (Gilbert 1966).

We monitored radio-tagged deer, elk, and moose for mortality signals 2-3 times/week during winter and spring and 1-2 times/week during summer and fall. When a mortality signal was received, the collar was located and the site and any remains were examined to determine cause of death. Mortality signals of radio-tagged animals were usually investigated 1-4 days after death. Predation was considered to be the cause of death when blood, subcutaneous hemorrhaging at wound sites, or sign of a struggle was found at the site. Evidence such as bear or wolf hair, tracks, scats and vomit, presence of buried carcass, and percent of carcass found was used to determine the species of predator responsible (O'Gara 1978). These data were incorporated into a key similar to that of Hatter (1984) to aid in ascertaining the type of predator involved. When evidence of 2 predators was found and we could not determine which predator had killed and which had scavenged, we classified the cause of mortality to a dual predator group.

We computed survival and cause-specific mortality rates via the program MICROMORT (Heisey 1985, Heisey and Fuller 1985); the biological year began on 1 June, the assumed birthdate of fawns/calves. Initially, each month was considered an interval with a constant daily survival rate. Daily survival rates for each interval were compared by log-likelihood ratio analysis, and data from intervals was pooled if rates were not significantly different (Heisey and Fuller 1985).

Signal loss from radio collars after the expected 3 year life of the battery was assumed to result from battery failure. We assumed battery failure in one deer's signal that disappeared after 802 days and in one elk's signal that disappeared after 930 days. We also assumed battery failure in one deer's signal that disappeared after only 160 days because the pulse rate of the collar doubled shortly after it was placed on the deer. Another signal disappeared from a radio that had only been out 23 days. This deer was included in analysis because it was found 2 years later while backtracking wolves to the animal's carcass.

Recruitment Rates (prediction 1a)

<u>Deer</u>.--

We conducted roadside counts of deer in open fields on approximately 10 evenings in late April and early May each year to estimate doe/fawn ratios and classify deer by sex. We drove a 13 km transect beginning one hour before sunset and counted and classified deer through a spotting scope. Doe:fawn ratios were compared among years with Mann Whitney <u>U</u> tests. We used Pearson correlation analysis to compare the number of does counted per evening with the number of days between the departure of snow from Polebridge and when the count was done to examine effects of phenology on the counts. We also estimated doe:fawn ratios by approaching radio-tagged does in late April and early May each year until we could confirm the number of fawns with each doe.

Elk.--

Elk were counted and classified by sex and age from a Cessna 182 along a survey route that was flown 5 times in January of 1991 and 1992 (Bureau 1992). A helicopter survey was flown each April from 1993-96. For this survey, the study area was stratified into subunits (19 low, 5 medium, and 5 high density subunits) as outlined by Unsworth et al. (1991). All elk visible to the pilot and 2 observers were counted and classified by sex and age in a sample of these subunits each year. Population estimates were computed via the computer program AERIAL SURVEY (Unsworth et al. 1991) which provided a sightability model for estimating the number of unseen elk. Mean elk population estimates were compared between years using 2-sample *t*-tests.

Moose.--

Four quadrants (3 large clearcuts and one 8-km^2 river bottom area) with relatively high moose densities were searched for moose by 3 observers in a Cessna 185 in December 1990 and January 1991 (Langley 1992). Flights were conducted at least 4 days apart and flown at 200 km/hr, 150 m above ground. Each area was searched until all visible moose were counted and classified. Six quadrants were searched during 2 flights in February 1992.

Helicopter surveys of all known moose winter range (420 km^2) on the British Columbia side of the Flathead were flown by British Columbia Ministry of Environment personnel on 3 consecutive days in January 1991 and on one day in December 1991. All moose seen were classified by sex and age.

In 1992-96 we located all radio-tagged moose on 3-5 flights each April with a Cessna 185 to determine the number of calves (short yearlings) with each cow. Only those moose for which we were confident about the presence/absence of a calf or calves were used in estimating the cow/calf ratio.

We estimated yearly population trend (lambda) of female deer, elk, and moose using the R/M equation of Hatter and Bergerud (1991):

lambda = $(1-\underline{M})/(1-\underline{R})$ where

$\underline{M} = \underline{d}/\underline{N}_0$, the finite annual adult mortality rate

$\underline{R} = \underline{r}/\underline{N}_1$, the finite annual recruitment rate = $\underline{R}$ = $(\underline{CC}/2)/(100+\underline{CC}/2)$ where $\underline{CC}$ = the number of fawns or calves per 100 females

Annual mortality rates were determined from the radio-tagged sample of adult females. Fawn/doe and calf/cow ratios were determined as described above. Confidence intervals for lambda were derived by combining confidence intervals computed for survival rates by MICROMORT and confidence intervals for fawn/doe and calf/cow ratios (from AERIAL SURVEY). Because we had no estimate of variance from our moose calf/cow surveys, we could not estimate confidence intervals for moose lambdas.

Pellet Trend (prediction 1b)

We counted deer, elk, and moose pellet-groups in 80 uncleared 1.8 m-radius plots on each of 11-17 pairs of transects during late April and early May each year. Most transects were initiated at 1.6 km intervals along Glacier Route 7. Plots were spaced at 50-m intervals along the transect (40 plots per transect) and paired transects were 200 m apart. Transects were distributed to encompass the entire range of habitat types and geographic variation in the area. Age of pellets was classified as "new" (< 1 month), "intermediate" (< 6 months), or old (> 6 months) based on color and sheen (Rachael 1992). Because pellet data were not normally distributed, the Kruskall-Wallis test was used to compare mean number of new and intermediate pellets/plot among years. Mann Whitney U tests were used to compare mean number of pellets/plot between years.

Hunter Success (predictions 1b and 2f)

We operated a hunter big game check station each year to estimate the age and sex composition of hunter-killed deer and elk and to estimate hunter effort and success to compare among years and to other check stations in areas without wolves. Correlation analysis was used to compare diastema lengths of yearling male deer killed by hunters with year to estimate trends in condition of deer. Mean diastema length of yearling male deer was compared with other hunting units in northwestern Montana by one-way ANOVA and Duncan multiple range post hoc tests. Hunter days/deer or elk harvested in the North Fork and in other hunting units in the northwestern region of Montana was correlated with year to estimate the trend in the deer and elk populations (Freddy 1982, Rooseberry and Woolf 1991). Pearson correlation analysis was also used to compare hunter days/deer or elk harvested with the total of daily snow depths for November of each year to examine effects of snow on hunter success.

Factors Affecting Mortality Rates

Age (prediction 2b)

We separated radio-tagged animals into classes to compare their respective survival rates with Z-tests (Heisey and Fuller 1985). Deer were pooled into age classes by 2-year intervals. Elk and moose were pooled into 3 age classes because of small sample size. The trend in survival rates resulting from pooling was similar to the unpooled trend (8 age classes). Median capture ages of deer, elk, and moose were compared to median ages of death by Mann-Whitney U tests.

Area (prediction 2c)

We compared via *Z*-tests survival rates of deer, elk, and moose among areas differing by presence of wolves and the presence of deer.

Nutritional condition (predictions 2d and 2f)

Femur marrow, when present, was collected from each carcass. These samples were double wrapped in plastic and kept frozen until they were weighed and then oven-dried at 60° C for 48 hours and reweighed. The dry weight of the marrow expressed as a percentage of its fresh weight was used to estimate percent fat (Neiland 1970). In addition to collections from radio-tagged animals, we collected femurs and estimated ages of cougar and wolf kills found by snowtracking and other methods described in chapter 1.

Following the methods of Gasaway et al. (1992) and Carbyn et al. (1993), we considered predation on deer < 10 yrs old (Nelson and Mech 1990), elk ≤ 12 yrs old (Houston 1982), and moose ≤ 15 yrs old (Gasaway et al. 1992) to be noncompensatory. Further, we considered predation on deer with FMF $> 25\%$ (Cheatum 1949), elk with $> 35\%$ FMF (Bubenik 1982), and moose with FMF $> 20\%$ (Peterson et al. 1984) to be noncompensatory.

Factors Explaining Cervid Population Trends (prediction 2e)

Pearson correlations and partial correlations were computed using stepwise multiple regression analysis to assess the relative contributions of snow depth, (number of days with > 30 cm snow on the ground; Fuller 1991a, Pauley et al. 1993), animal condition (% femur marrow fat of deer killed by cougars and wolves), diastema lengths of yearling male deer, and minimum number of wolves present in May (estimated as described by Pletscher et al. [1997]), to elk and deer population trends as estimated by hunter success. We thereby tested for the effect of limiting factors while controlling for the effect of other, potentially confounding factors. This procedure is similar to a key-factor analysis (Varley and Gradwell 1960, Messier 1994). Pearson correlations were used to associate annual deer survival rates, annual elk survival rates, and annual moose survival rates to one another and to the number of days with > 30 cm of snow on the ground, and to compare mean femur marrow fat values (of deer killed by cougars and wolves) with total number of days with > 30 cm snow on the ground and years. Pearson correlation was also used to examine association between the annual bear-caused mortality rate on moose and production of bear foods including huckleberry (Vaccinium globulare), serviceberry (Amelanchier alnifolia), and (Shepherdia canadensis). Production was estimated by transects sampled yearly as described by Kasworm and Servheen (1995).

RESULTS

Survival Rates (predictions 1a and 2a)

We radio-tagged 67 female deer, 55 female elk, and 49 female moose. Median estimated capture age was 4.5 years (range, 0.5 - 13.5 years) for deer, 6.5 years (range, 0.5 - 15.5) for elk, and 6.5 years (range 1.5 - 14.5 years) for moose.

Three radio-tagged deer were excluded from the survival analysis; 1 radio collar was removed because the deer became habituated to humans, and we suspected capture myopathy (Harthoorn 1977) in the other 2 deer that died within 12 days of capture. Two radio-tagged elk were excluded from the survival analysis; 1 as a result of capture-related mortality and 1 due to disappearance of the signal the day after it was captured. Two moose were excluded from survival analysis due to capture-related mortalities and 2 were excluded due to dropped collars.

Daily mortality rates for deer during August and September were significantly higher than all other months (Z test, $P < 0.05$), therefore 3 intervals were defined where survival was constant: June-July, August-September, and October-May (Fig 1). Forty-two (66%) deer died during the study period resulting in an overall yearly survival rate of 0.74 (Table 1)

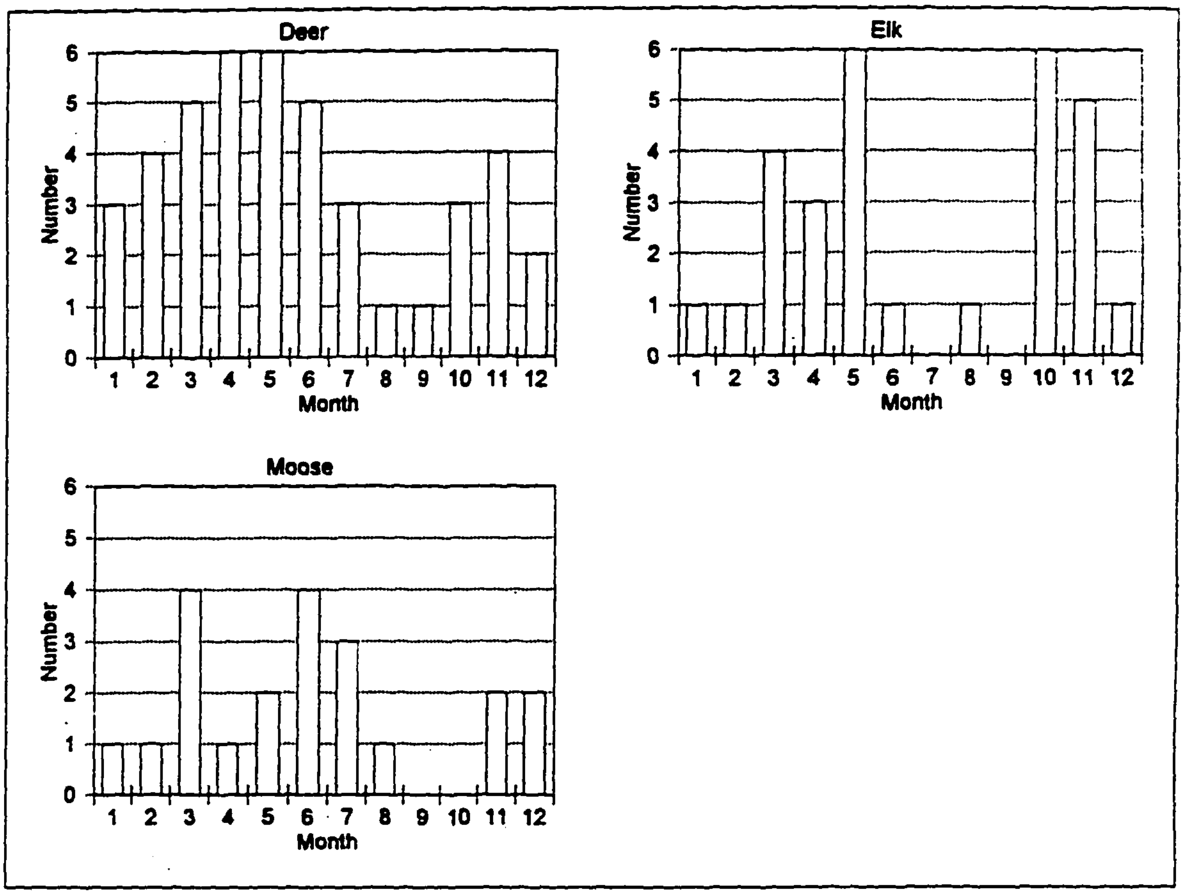

Figure 1. Monthly mortality rates for radio-tagged White-tailed deer, elk, and moose in and near Glacier National Park, 1990-1996.

Table 1. Age-specific and yearly survival rates of white-tailed deer in and near Glacier National Park, Montana for January 1990 through June 1996.

	June-July			August-September		
Class	n[1]	rate	95% CI	n[1]	rate	95% CI
≤ 2 yrs	636	1.00	1.00-1.00	610	1.00	1.00-1.00
3-6 yrs	3,414	0.98	0.95-1.00	3,337	0.98	0.95-1.00
≥ 7 yrs	3,276	0.89	0.82-0.98	3,083	1.00	1.00-1.00
1991	1,201	0.86	0.72-1.00	1,159	1.00	1.00-1.00
1992	1,490	1.00	1.00-1.00	1,464	1.00	1.00-1.00
1993	1,342	1.00	1.00-1.00	1,342	1.00	1.00-1.00
1994	1,483	0.96	0.89-1.00	1,385	0.96	0.88-1.00
1995	1,433	0.92	0.82-1.00	1,342	1.00	1.00-1.00
1996	1,353	0.96	0.87-1.00	1,258	0.95	0.87-1.00
All	8,302	0.94	0.91-0.98	7,950	0.98	0.96-1.00

Table 1. Continued.

	October-May			Annual[2]	
	n[1]	rate	95% CI	rate	95% CI
≤ 2 yrs	5,524	0.77	0.62-0.95	0.77	0.62-0.95
3-6 yrs	13,656	0.73	0.63-0.84	0.70	0.60-0.82
≥ 7 yrs	9,384	0.81	0.70-0.94	0.73	0.61-0.86
1991	6,030	0.72	0.58-0.91	0.62	0.47-0.82
1992	5,517	0.84	0.71-1.00	0.84	0.71-1.00
1993	6,174	0.76	0.62-0.93	0.76	0.62-0.93
1994	5,805	0.78	0.64-0.95	0.71	0.57-0.90
1995	5,857	0.78	0.64-0.95	0.72	0.57-0.90
1996	3,698	0.88	0.73-1.00	0.80	0.64-1.00
All	33,081	0.80	0.74-0.86	0.74	0.68-0.80

[1] radiodays

[2] _n_ = 49,333

For elk, the daily survival rate in October was significantly lower than the September rate and the December rate was higher than the November rate while the March rate was lower than the February rate (Z test, $P < 0.05$; Fig. 1). Therefore, 4 intervals were defined where survival was constant: June-September, October-November, December-February, and March-May. Twenty-eight (53%) elk died during the study period resulting in an overall yearly survival rate of 0.83 (Table 2).

For moose, the daily survival rate in June was significantly lower than the September and November rates and the March rate was lower than the November rate ($P < 0.05$; Fig. 1). Therefore, 4 intervals were defined where survival was constant: June-July, August-October, November-February, and March-May. Twenty-one (47%) moose died during the study period resulting in an overall yearly survival rate of 0.88 (Table 3).

Recruitment and Rate of Change (prediction 1a)

Doe/fawn ratios obtained from roadside counts were similar to ratios obtained from radio-tagged does (1994: 25.4 vs 30.0, 1995: 31.9 vs 37.0, 1996: 30.4 vs 33.0, respectively). Based on roadside counts, doe/fawn ratios in 1993 and 1994 were significantly lower than counts in 1990 (Mann Whitney $U = 26.0$, $P = 0.024$; Mann Whitney $U = 32.0$, $P = 0.036$, respectively; Table 4). The rate of change (λ) for

Table 2. Age-specific and yearly survival rates of elk in and near Glacier National Park, Montana for January 1990 through June 1996.

	June-September			October-November			December-Feb		
Class	n^1	rate	95% CI	n^1	rate	95% CI	n^1	rate	95% CI
≤ 2 yrs	1,318	1.00	1.00-1.00	576	0.90	0.73-1.00	1,004	0.76	0.56-1.00
3-7 yrs	6,222	1.00	1.00-1.00	3,001	0.94	0.88-1.00	5,485	1.00	1.00-1.00
≥ 8 yrs	9,368	0.97	0.94-1.00	4,401	0.91	0.84-0.98	7,416	0.97	0.94-1.00
1991	1,586	1.00	1.00-1.00	722	0.84	0.67-1.00	2,216	0.89	0.77-1.00
1992	2,806	1.00	1.00-1.00	1,369	0.96	0.88-1.00	2,333	0.96	0.89-1.00
1993	2,928	1.00	1.00-1.00	1,391	0.96	0.88-1.00	2,277	0.96	0.89-1.00
1994	3,178	0.96	0.89-1.00	1,512	0.89	0.77-1.00	2,483	1.00	1.00-1.00

Table 2. Continued

1995	3,294	1.00	1.00-1.00	1,594	0.93	0.83-1.00	2,278	1.00	1.00-1.00
1996	3,116	0.96	0.89-1.00	1,390	0.92	0.81-1.00	2,002	1.00	1.00-1.00
All	16,908	0.99	0.97-1.00	7,978	0.92	0.87-0.97	13,634	0.97	0.94-1.00

	March-May			Annual[2]	
	n[1]	rate	95% CI	rate	95% CI
≤ 2 yrs	1,276	0.87	0.71-1.00	0.59	0.39-0.90
3-7 yrs	6,063	0.98	0.96-1.00	0.93	0.86-1.00
≥ 8 yrs	7,891	0.91	0.85-0.97	0.79	0.71-0.88
1991	2,319	0.85	0.73-1.00	0.64	0.47-0.88
1992	2,213	0.96	0.88-1.00	0.88	0.77-1.00
1993	2,563	0.96	0.90-1.00	0.89	0.77-1.00

Table 2. Continued

1994	2,562	0.96	0.90-1.00	0.82	0.69-0.98
1995	2,440	0.96	0.89-1.00	0.89	0.78-1.00
1996	1,961	0.95	0.87-1.00	0.84	0.72-0.98
All	14,058	0.94	0.91-0.98	0.83	0.77-0.89

[1] radiodays

[2] n = 52,578

Table 3. Age-specific and yearly survival rates of moose in and near Glacier National Park, Montana for January 1990 through June 1996.

	June-July			August - October			November-Feb		
Class	n^1	rate	95% CI	n^1	rate	95% CI	n^1	rate	95% CI
≤ 3 yrs	236	0.77	0.46-1.00	276	1.00	1.00-1.00	811	1.00	1.00-1.00
3-10 yrs	6,305	0.98	0.95-1.00	9,371	1.00	1.00-1.00	14,035	0.98	0.96-1.00
≥ 11 yrs	3,055	0.92	0.85-1.00	4,421	0.98	0.94-1.00	5,860	0.92	0.85-1.00
1991	1,271	0.91	0.80-1.00	1,748	1.00	1.00-1.00	3,122	1.00	1.00-1.00
1992	1,732	0.97	0.90-1.00	2,576	1.00	1.00-1.00	3,388	1.00	1.00-1.00
1993	1,696	0.96	0.90-1.00	2,484	1.00	1.00-1.00	3,047	0.92	0.83-1.00
1994	1,410	0.96	0.88-1.00	2,103	1.00	1.00-1.00	3,478	0.97	0.90-1.00

Table 3. Continued

1995	1,893	0.97	0.91-1.00	2,765	0.97	0.91-1.00	3,544	0.97	0.90-1.00
1996	1,594	0.96	0.89-1.00	2,392	1.00	1.00-1.00	2,995	0.92	0.83-1.00
All	9,596	0.96	0.92-0.99	14,068	0.99	0.98-1.00	19,574	0.97	0.94-0.99

	March-May			Annual[2]	
	n[1]	rate	95% CI	rate	95% CI
≤ 3 yrs	920	1.00	1.00-1.00	0.77	0.46-1.00
3-10 yrs	11,823	0.96	0.93-1.00	0.93	0.88-0.97
≥ 11 yrs	4,386	0.96	0.90-1.00	0.80	0.70-0.91
1991	2,682	0.97	0.90-1.00	0.88	0.76-1.00
1992	2,576	1.00	1.00-1.00	0.97	0.90-1.00
1993	2,225	0.96	0.88-1.00	0.85	0.73-0.98

Table 3. Continued

1994	2,969	0.97	0.91-1.00	0.90	0.79-1.00
1995	2,651	0.93	0.85-1.00	0.84	0.73-0.98
1996	2,063	0.91	0.81-1.00	0.81	0.68-0.98
All	15,166	0.96	0.94-0.99	0.88	0.84-0.93

[1] radiodays

[2] $\underline{n}$ = 40,404 radiodays

Table 4. Population trend indices for white-tailed deer from 1986-1996 in and near Glacier National Park, Montana.

Year	Hunter days/deer	$\bar{x}$ pellets /plot[1,2]	fawns:doe[3]	lambda[4]
1986	12.6			
1987	19.9			
1988	27.8			
1989	22.7			
1990	27.7	0.46 (0.04)	0.392 (0.046)	
1991	19.7	0.32 (0.04)	0.344 (0.034)	0.75 (0.53-0.99)
1992	24.4	0.29 (0.04)	0.332 (0.017)	0.98 (0.81-1.18)
1993	28.6	0.37 (0.05)	0.248 (0.023)	0.84 (0.68-1.07)
1994	38.5	0.16 (0.02)	0.254 (0.031)	0.80 (0.62-1.04)
1995	24.9	0.16 (0.02)	0.319 (0.019)	0.82 (0.65-1.06)
1996	55.8	0.11 (0.02)	0.304 (0.026)	0.92 (0.72-1.18)

[1] 480 plots

[2] SE in parentheses

[3] SE in parentheses

[4] 95% CI in parentheses

the deer population was less than 1.0 for all years (Table 4).

The rate of change (λ) for elk was less than 1.0 for all years (Table 5). The rate of change (λ) for moose was greater than 1.0 before 1994 but was less than 1.0 for 1995 and 1996 (Table 6).

Pellet and Aerial Counts (prediction 1b)

The mean number of deer pellets/plot declined from 1990 (0.46, n = 480; Table 4) to 1992 (0.29; Mann Whitney U = 101461.5, P < 0.001) and from 1992 to 1994 (0.16; Mann Whitney U = 108465.0, P = 0.01). The decline from 1994 to 1996 was not significant (0.11; P = 0.447). The trend was similar for 960 plots counted annually.

The mean number of elk pellets/plot increased from 1991 (0.08, n = 960; Table 5) to 1993 (0.18 Mann Whitney U = 421938, P < 0.001) and declined from 1993 to 1996 (0.11 Mann Whitney U = 420516.5, P = 0.003).

Based on helicopter surveys, the estimated number of elk in the core study area was lower in 1994 (287) and 1996 (396) than 1993 (619; P < 0.0001, P = 0.09, respectively; Table 5).

Hunter Success (prediction 1b)

The number of hunter-days/deer harvested increased from 1990 to 1996 (r = 0.76, P = 0.004; Table 4). The number of

Table 5. Population trend indices for elk from 1986-1996 in and near Glacier National Park, Montana.

Year	Hunter-days/elk	count[1]	pellets/plot[2]	calves:cow[3]	lambda
1986	34.9				
1987	38.9				
1988	73.9				
1989	73.5				
1990	151.1				
1991	82.7		0.08	0.414	0.77
			(0.01)	(0.078)	(0.55-1.10)[4]
1992	85.8		0.12	0.163	0.97
			(0.01)	(0.016)	(0.82-1.09)
1993	228.6	619	0.18	0.116	0.94
		(122)	(0.02)	(0.007)	(0.81-1.07)
1994	113.3	287	0.06	0.142	0.88
		(34)	(0.01)	(0.033)	(0.73-1.07)
1995	107.2	382	0.09	0.160	0.96
		(106)	(0.01)	(0.052)	(0.82-1.11)
1996	260.2	396	0.11	0.134	0.90
		(183)	(0.01)	(0.040)	(0.75-1.07)

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[1] From spring helicopter survey, 90% CI in parentheses

[2] 960 plots , SE in parentheses

[3] From spring helicopter survey, except 1991 and 1992 which were from airplane, 90% CI in parentheses (95% for 1991, 1992)

[4] lambda 95% CI

Table 6. Population trend indices for moose from 1991-1996 in and near Glacier National Park, Montana.

Year	calves:cow[a]	lambda
1991	0.25	0.99
1992	0.22	1.07
1993	0.44	1.04
1994	0.30	1.03
1995	0.10	0.89
1996	0.09	0.85

[a] based on calves seen with radio-tagged cows during spring except 1995 and 1996 which was ratio of all calves and cows seen from the air in December.

hunter-days/elk harvested also increased from 1991 to 1996 (r = 0.69, P = 0.01; Table 5).

Cause-specific Mortality Rates (prediction 2a)

Cougar predation was the most common cause of mortality in deer accounting for 14 deaths (33%; Table 7). Wolf predation resulted in 10 deaths. Although mortality peaked during late winter and spring, rates remained relatively constant throughout the year except during August and September when they were especially low (Fig. 1).

Cougar predation was also the most common cause of mortality in elk, accounting for 12 deaths (43%; Table 8). Elk mortality rates were highest from March-May and in October-November (Fig. 1).

Wolf and bear predation were the most common causes of mortality in moose, each accounting for 5 deaths (24% each; Table 9). Moose mortality rates were highest in March and in June-July (Fig. 1).

Factors Affecting Mortality

Age (prediction 2b)

The annual survival rate was lower for 4-5 yr old deer (0.57) than the annual survival rate for 2-3 yr old deer (0.85; Z = 2.57, P = 0.01). Survival rates were similar when ages were grouped into 3 classes ($\leq$ 2, 3-6, $\geq$ 7 yrs; P > 0.10; Table 1).

Table 7. Cause-specific mortality rates of white-tailed deer in and near Glacier National Park, Montana for January 1990 through June 1996.

	June-July			August-September		
Source	n^1	rate	95% CI	n^1	rate	95% CI
Wolves	8,302	0.01	0.00-0.02	7,950	0.00	0.00-0.02
Humans		0.01	0.00-0.02		1.00	1.00-1.00
Bears		0.00	0.00-0.02		0.00	0.00-0.00
Cougars		0.02	0.00-0.05		0.00	0.00-0.00
Coyotes		0.00	0.00-0.00		0.00	0.00-0.00
Wolf/Cougar		0.01	0.00-0.02		0.00	0.00-0.00
Unknown Pred.		0.00	0.00-0.00		0.00	0.00-0.00
Old age		0.00	0.00-0.00		0.00	0.00-0.00
Unknown		0.00	0.00-0.00		0.00	0.00-0.00

Table 7. Continued.

	October-May			Annual[2]		
	n[1]	rate	95% CI	n[1](%)	rate	95% CI
Wolves	33,081	0.05	0.02-0.08	10(24)	0.06	0.03-0.10
Humans		0.03	0.00-0.05	5(12)	0.03	0.00-0.06
Bears		0.01	0.00-0.03	4(10)	0.03	0.00-0.05
Cougars		0.07	0.03-0.11	14(33)	0.09	0.04-0.13
Coyotes		0.01	0.00-0.03	2(05)	0.01	0.00-0.03
Wolf/Cougar		0.00	0.00-0.00	1(02)	0.01	0.00-0.01
Unknown Pred.		0.01	0.00-0.03	2(05)	0.01	0.00-0.03
Old age/pneum.		0.01	0.00-0.02	1(02)	0.01	0.00-0.02
Unknown		0.02	0.00-0.04	3(07)	0.02	0.00-0.04

[1] radiodays

[2] *n* = 49,333

Table 8. Cause-specific mortality rates of elk in and near Glacier National Park, Montana for January 1990 through June 1996.

	June-September			October-November			December-Feb		
Source	n[1]	rate	95% CI	n[1]	rate	95% CI	n[1]	rate	95% CI
Cougar	16,908	0.00	0.00-0.00	7,978	0.01	0.00-0.03	13,634	0.01	0.00-0.03
Human		0.00	0.00-0.00		0.04	0.01-0.07		0.01	0.00-0.02
Wolf		0.00	0.00-0.00		0.01	0.00-0.03		0.01	0.00-0.02
Grizzly		0.01	0.00-0.03		0.00	0.00-0.00		0.01	0.00-0.02
Bear/wolf		0.00	0.00-0.00		0.01	0.00-0.02		0.00	0.00-0.00
Unknown		0.00	0.00-0.00		0.01	0.00-0.02		0.00	0.00-0.00

Table 8. Continued

	March-May			Annual[2]		
	n[1]	rate	95% CI	n(%)	rate	95% CI
Cougar	14,058	0.04	0.01-0.07	12(43)	0.06	0.02-0.10
Human		0.00	0.00-0.00	6(21)	0.04	0.01-0.08
Wolf		0.01	0.00-0.02	3(11)	0.03	0.00-0.05
Grizzly		0.00	0.00-0.00	3(11)	0.02	0.00-0.04
Bear/wolf		0.01	0.00-0.03	3(11)	0.02	0.00-0.04
Unknown		0.00	0.00-0.00	1(04)	0.01	0.00-0.02

[1] radiodays

[2] _n_ = 52,578 radiodays

Table 9. Cause-specific mortality rates of moose in and near Glacier National Park area, Montana for January 1990 through June 1996.

	June-July			August-October			November-Feb		
Source	n[1]	rate	95% CI	n[1]	rate	95% CI	n[1]	rate	95% CI
Grizzly	9,596	0.02	0.00-0.04	14,068	0.00	0.00-0.00	19,574	0.00	0.00-0.00
Wolf		0.01	0.00-0.02		0.00	0.00-0.00		0.01	0.00-0.03
Human		0.00	0.00-0.00		0.00	0.00-0.00		0.01	0.00-0.03
Bear		0.01	0.00-0.02		0.00	0.00-0.00		0.00	0.00-0.00
Unknown		0.01	0.00-0.02		0.00	0.00-0.00		0.00	0.00-0.00
Bear/wolf		0.01	0.00-0.02		0.00	0.00-0.00		0.00	0.00-0.00
Accident		0.00	0.00-0.00		0.00	0.00-0.00		0.00	0.00-0.00
Unknown Pred.		0.00	0.00-0.00		0.00	0.00-0.00		0.00	0.00-0.00
Injury/pneum.		0.00	0.00-0.00		0.00	0.00-0.00		0.01	0.00-0.02

Table 9. Continued.

	March-May			Annual[2]		
	n[1]	rate	95% CI	n(%)	rate	95% CI
Grizzly	15,166	0.01	0.00-0.02	5(24)	0.03	0.00-0.06
Wolf		0.01	0.00-0.03	5(24)	0.03	0.00-0.05
Human		0.00	0.00-0.00	3(14)	0.02	0.00-0.04
Bear		0.01	0.00-0.02	2(10)	0.01	0.00-0.03
Unknown		0.01	0.00-0.02	2(10)	0.01	0.00-0.03
Bear/wolf		0.00	0.00-0.00	1(05)	0.01	0.00-0.02
Accident		0.01	0.00-0.02	1(05)	0.01	0.00-0.02
Unknown Pred.		0.01	0.00-0.02	1(05)	0.01	0.00-0.02
Injury/pneum.		0.00	0.00-0.00	1(05)	0.01	0.00-0.02

[1] radiodays

[2] n = 40,404 radiodays

The median age of deer killed by cougars (6.5, n = 12) was greater than the median capture age of deer (4.5, n = 58, Mann-Whitney U = 211.5, P = 0.03). No difference between the median capture age of deer and the median age of deer killed by wolves was apparent (4.5, n = 9, Mann-Whitney U = 240.0, Z = 0.389, P = 0.697).

The annual survival rate of elk $\leq$ 2 yrs (0.59) was lower than the annual survival rate for elk 3-7 yrs (0.93; Z = 2.50, P = 0.012; Table 2). The annual survival rate for elk 3-7 yrs was greater than the rate for elk $\geq$ 8 (0.79, Z = 2.50, P = 0.012).

The median age of elk killed by cougars (10.3, N = 12) was greater than the median capture age of elk (6.5, n = 55, Mann-Whitney U = 210.0, Z = -1.97, P = 0.05). The cougar-caused mortality rate on elk $\leq$ 2 yrs (0.23) was greater than the cougar-caused mortality rate on 3-7 yr old elk (0.01; Z = 2.09, P = 0.037). The cougar-caused mortality rate on elk $\geq$ 8 (0.07) was greater than the rate on 3-7 yr old elk (Z = 2.00, P = 0.046). Wolf-caused mortality rates were not different among $\leq$ 2 yr old elk (0.07), 3-7 yr old elk (0.02) or $\geq$ 8 yr old elk (0.02; Z = 0.71, P > 0.10). The grizzly-caused mortality rate was marginally greater on $\geq$ 8 yr old elk (0.04) than on 3-7 yr old elk (0.00; Z = 1.71, P = 0.087).

The median age of moose killed by all predators combined (10.8, n = 22) was greater than the median capture age of moose (6.5, N = 49; Mann-Whitney $\underline{U} = 284.5$, $\underline{P} = 0.002$).

Moose 11-17 yrs old had a lower survival rate (0.80) than moose 3-10 yrs old (0.93, $\underline{Z} = 2.17$, $\underline{P} = 0.03$; Table 3). Bear and wolf-caused mortality rates were not significantly correlated with age ($\underline{P} > 0.10$).

Area (prediction 2c)

Survival rates during winter were similar among deer wintering on the Bowman (0.87, $\underline{n} = 15$), Kintla (0.91, $\underline{n} = 16$), or Logging winter ranges (0.90, $\underline{n} = 21$; $\underline{P} > 0.10$). Only 2 deer were killed by wolves on the Kintla and Logging winter ranges while 6 deer were killed by cougars.

The survival rate of deer during summer ranges where wolves were absent (0.94, $\underline{n} = 5$) was higher, but not significantly, than the rate on summer ranges where wolves were present (0.87, $\underline{n} = 51$; $\underline{Z} = 1.02$, $\underline{P} = 0.31$).

The survival rate of elk on summer ranges where wolves were not present (0.95, $\underline{n} = 5$) was not different than the survival rate on ranges where wolves were present (0.97, $\underline{n} = 40$; $\underline{Z} = 0.36$, $\underline{P} = 0.72$).

The November-February interval survival rate of moose living in wolf territories (0.90, $\underline{n} = 25$) was significantly lower than the interval survival rate for moose outside wolf territories (1.00, $\underline{n} = 13$, $\underline{Z} = 2.58$, $\underline{P} = 0.01$). The annual survival rate for moose living in wolf territories (0.82, $\underline{n} = 25$) was lower, but not significantly, than the rate of moose outside wolf territories (0.90, $\underline{n} = 13$, $\underline{Z} = 1.35$, $\underline{P} = 0.18$).

The wolf-caused mortality rate for moose in areas without wintering deer (0.08, $\underline{n} = 13$) was significantly greater than that for moose in areas with wintering deer (0.00, $\underline{n} = 4$; $\underline{Z} = 2.09$, $\underline{P} = 0.037$).

Additive vs Compensatory Mortality (prediction 2d)

Thirty-four of 38 (89%) deer killed by predators were ≤ 10 yrs old. The mean FMF of deer killed by predators was 67.1% (range = 6.3% - 95.0%). Only one deer killed by predators had a FMF < 25%. Twenty of 29 (69%) radioed elk killed by predators were ≤ 12 yrs old. The mean FMF of predator-killed elk was 59.9% (range = 17.4% - 92.1%). Only one elk killed by predators had FMF level < 35%. Sixteen of 21 cows (76%) killed by predators in our study were ≤ 15 yrs. The mean femur marrow fat of moose killed by predators was 73.6% (range = 40.9% - 89.4%).

Ninety-two percent of all non-radioed deer and 94% of all non-radioed moose killed by wolves and cougars since 1986 had FMF values > 20% ($\bar{x} = 71.4\%$, 64.6%, respectively). Ninety-five percent of elk killed during the same period had FMF values > 35% ($\bar{x} = 71.1$).

Ninety-three percent of all non-radioed deer and 90% of all non-radioed elk and moose killed by wolves and cougars since 1986 were younger than 10, 12, and 15 years respectively.

Wolf-caused and cougar-caused annual mortality rates for deer were not correlated (_r_ = 0.029, _P_ = 0.96) possibly indicating an additive predation effect.

Factors Explaining Declines (prediction 2e)

Deer

Annual survival rates were negatively correlated with the number of days per winter with > 30 cm of snow on the ground (_r_ = 0.72, _P_ = 0.06). Hunter-days/deer harvested (deer population trend) was not significantly correlated with total snow depth during the November hunting season (_r_ = -0.067, _P_ = 0.85, _n_ = 11). Hunter-days/deer harvested was correlated with hunter-days/elk harvested (_r_ = 0.788, _P_ = 0.004, _n_ = 11) and marginally with wolf numbers (_r_ = 0.529, _P_ = 0.094, _n_ = 11). There was no correlation between hunter-days/deer harvested and number of days per winter with > 30 cm snow (_r_ = -0.296, _P_ = 0.376, _n_ = 11) or mean femur marrow fat content of deer killed by wolves and cougars (_r_ = -0.117, _P_ = 0.802, _n_ = 7) or mean diastema length of yearling male deer killed by hunters (_r_ = 0.264, _P_ = 0.43, _n_ = 11). When snow depth and diastema length were controlled for, hunter days/deer harvested was marginally correlated with wolf numbers (_r_ = 0.53, _P_ = 0.09).

Elk

Annual survival rates of elk were not correlated with the number of days per winter with > 30 cm of snow on the ground ($r = 0.41$, $P = 0.42$). Annual elk survival rates were marginally correlated with annual deer survival rates ($r = 0.78$, $P = 0.068$).

Annual cougar-caused mortality rates on elk declined from 1991 through 1996. The rate for 1991-93 (0.12) was significantly higher than the rate for 1994-96 (0.01; $Z = 2.72$, $P = 0.007$). The annual wolf-caused mortality rates on elk did not differ among years ($Z = 1.46$, $P = 0.14$).

There was no significant relationship between hunter-days/elk harvested (elk population trend) and depth of snow in November ($r = -0.358$, $P = 0.917$). Hunter-days/elk harvested was correlated with wolf numbers ($r = 0.576$, $P = 0.064$, $n = 11$) and hunter-days/deer harvested ($r = 0.788$, $P = 0.004$, $n = 11$). There was no correlation between hunter-days/elk harvested and number of days per winter with > 30 cm snow (0.049, $P = 0.89$, $n = 11$). When snow depth was controlled for hunter days/elk harvested was marginally correlated with wolf numbers ($r = 0.58$, $P = 0.08$).

Moose

Annual survival rates of moose were not correlated with the number of days per winter with > 30 cm of snow on the ground ($r = 0.32$, $P = 0.55$). The annual bear-caused mortality rate on moose was greater in 1995 (0.09) than in 1992 (0.00) and 1994 (0.00; $Z = 1.66$, $P = 0.097$; $Z = 1.82$, $P = 0.069$, respectively). The annual survival rates were positively correlated with the mean annual production of serviceberry in northwestern Montana ($r = 0.94$, $P = 0.005$).

North Fork vs Regional Trends (prediction 2f)

Deer

In contrast to our study area, hunter-days/deer harvested in northwest Montana were significantly correlated with year, declining from 1987 to 1995 ($r = -0.71$, $P = 0.031$).

The mean diastema length of yearling males brought through the North Fork check station from 1992-1996 (70.7 mm, SE = 0.9, $n = 33$) was higher than any of the 6 hunting unit check stations in northwestern Montana and it was significantly higher than the mean from 2 of these check stations (Olney: $\bar{x} = 67.9$, SE = 0.3, $n = 272$, Duncan multiple range $P < 0.05$; Swan Valley: $\bar{x} = 68.0$, SE = 0.3, $n = 376$, Duncan multiple range $P < 0.05$). The mean diastema length of yearling males in 1995 for all check stations in northwestern Montana combined (68.5 mm, SE = 0.27, $n = 235$) was less than the mean for 1985 (71.2 mm, SE = 1.0, $n = 25$; $t = 3.06$, 258 df, $P = 0.002$). The sample size of diastemas from the North Fork was too small for comparison by t test, however, we found no correlation between year and diastema length of yearling males ($r = 0.129$, $P = 0.141$).

Mean femur marrow fat (FMF) of deer killed by wolves and cougars in the North Fork was not correlated with years from 1989-1996 (r = - 0.316, P = 0.49), but was marginally negatively correlated with annual total snow depth (r = - 0.69, P = 0.08).

Elk

Hunter-days/elk harvested in northwest Montana did not change significantly from 1987-1995 (r = 0.16, P = 0.67). The sample size of diastema from yearling male elk from the North Fork check station was too small to compare with other check stations in northwestern Montana. Femur fat values for all elk killed by cougars and wolves in the North Fork have not changed from 1986 to 1996 (r = -0.134, P = 0.25).

DISCUSSION

Survival Rates

We did not find published estimates of deer, elk, or moose survival rates in areas with a complement of predators equivalent to the one found in our study area. The annual survival rate of deer in our study area (0.74) was similar to the survival rate reported for black-tailed deer (*Odocoileus hemionus*) on Vancouver Island (0.74) where wolves, cougars, humans, coyotes, and black bears were present (McNay and Voller 1995). Wolf-caused mortality rates on deer (0.06) and cougar-caused mortality rates on deer (0.09) in our study area were also similar to those reported on Vancouver Island (0.07 and 0.08, respectively). The survival rate of white-tailed deer was 0.79 in northeastern Minnesota (Nelson and Mech 1986) and 0.69 in northcentral Minnesota (Fuller 1990). The wolf-caused mortality rate in the North Fork was lower than the wolf-caused mortality rate reported in northeastern Minnesota (0.17) where the deer:wolf ratio was (35:1; Fuller 1989) was higher than the deer:wolf ratio in the NF (approximately 250:1; K. Kunkel, unpubl. data) but higher than the wolf-caused mortality rate in northcentral Minnesota (0.04) where the wolf:deer ratio was 140:1 (Fuller 1989).

Deer mortality rates were relatively high throughout the year except during August-September when they were very low. Similar to rates reported by Nelson and Mech (1986), Fuller (1990), and McNay and Voller (1995), rates peaked during late winter and early spring. Unlike these studies, our monthly mortality rates remained high through July. This may have resulted from the wider array of predators killing deer in our study area.

The survival rate of female elk in our study (0.83) falls within the range found in other studies (0.78 - 0.92; White 1985, Freddy 1987, Leptich and Zager 1991, Unsworth et al. 1993, Coughenour and Singer 1996). Non-human predators were not responsible for any of the mortalities in those studies [Coughenour and Singer (1996) did not indicate causes of mortality]; mortality was almost exclusively human-caused during the fall hunting season. We are aware of no published studies documenting predation as more than an incidental mortality factor on radio-tagged elk despite the fact that Hornocker (1970), Murphey et al. (1992), and Williams et al. (1995) have reported that elk may make up a large part of the diet of cougars.

Annual survival rates of moose in our study (0.88) were slightly lower than rates reported by Larsen et al. (1989) in Yukon (0.91) and Bangs et al. (1989) in Kenai, Alaska (0.92). Bears and wolves killed less than 4% of adult females annually in these studies. Wolves killed 7% of adult female moose annually in Alberta (Hauge and Keith 1981) and a similar percentage in south-central Alaska (Gasaway et al. 1983). Only our study and that of Gasaway et al. (1983) found bears and wolves to be the most important causes of mortality. Most of the bear-caused mortality in our study occurred from May-August. Larsen et al. (1989) and Boertje et al. (1988) reported that most moose mortality in their studies occurred during spring and speculated that cows may be most vulnerable to predators during calving because of reduced mobility and because they defend newborn calves. Cows in our study were also vulnerable to wolves during late winter, similar to the findings of Peterson (1977) and Peterson et al. (1984).

Population Trends

While we acknowledge the potential problems of the individual trend indices we used (e.g. pellet counts; Fuller 1991*b*), all of them (pellet counts, survival and recruitment rates, hunter success rates, diastema length) showed similar trends strongly suggesting that deer declines were both significant and real. Trends were slightly less clear for elk. Elk distribution during winter in our study area is more affected by winter severity than is deer distribution (Bureau 1992, Rachael 1992). As a result, distribution of elk pellets probably varies more among winters than does distribution of deer pellets and this may obscure the population trend. The number of days between snow departure from the valley floor and the date of our helicopter survey for elk varied from 9 to 36 days. The number of elk using open areas and not migrating out of the survey area probably differs over this interval and may have affected population estimates. Additionally, the number of subunits with low densities of elk that we surveyed by helicopter each year was less than that recommended by Unsworth et al. (1991). Despite the lack of clear agreement among the indices, it is difficult to envision anything but a declining population with our elk survival rates combined with such consistently low calf:cow ratios.

White-tailed deer and elk populations increased from 1986 through 1996 in all areas of northwestern Montana except the North Fork (NF). The decline of deer and elk in the NF was marginally correlated with the increase in wolf numbers following recolonization. The deer decline was not correlated with snow depths or deer condition as indexed by diastema length. The elk decline was not correlated with snow depths but sample sizes were too small to examine elk condition parameters. Similar declines in deer abundance have been recorded after increases in wolf abundance in northeastern Minnesota (Messier 1991, Mech and Karns 1977) and on Vancouver Island (Hebert et al 1982). Wolves were identified as the primary limiting factor on deer recruitment on Vancouver Island (Janz and Hatter 1986), while winter severity and habitat changes combined with wolves resulted in the deer decline in Minnesota (Mech and Karns 1977).

Based on trends in human-caused cougar mortalities and cougar/human interactions, cougar numbers probably increased throughout Montana including the NF over the same period that wolves increased (Aune and Schladweiler 1995). The overall and area-specific magnitude of this trend is difficult to estimate. Had we had data on cougar population trends in the NF over the entire course of our study, we might have also found a correlation between that trend and deer and elk population trends because cougar-caused mortality rates on deer and elk were higher than wolf-caused mortality rates. Hornocker (1970) suggested that cougars were unlikely to greatly impact prey population trends by themselves. Increasingly, however, cougars have been shown to have significant limiting effects on ungulate populations. Cougars were the most important source of mortality on radio-tagged mule deer fawns in the central Sierra Nevada region of southern California (Neal 1990). Neal (1985) suggested that elimination of cougar predation alone (assuming all other factors remained the same) would reverse the downward trend in the deer population. Cougars were a primary cause of mortality in radio-tagged deer on Vancouver Island and McNay and Voller (1995:142) concluded that cougars had "strong local effects" on deer. Cougar predation caused populations of bighorn sheep (Ovis canadensis) to decline to low densities in 2 mountain ranges in California (Wehausen 1996). Wolves and cougars are the 2 top predators in North America; their potential to together limit ungulate populations is probably even greater than the combined effects of wolves and bears. Additional research on this topic is greatly needed.

In addition to wolves and cougars, grizzly bear numbers also increased in our study area. The finite rate of increase from 1979 to 1994 was 1.085 (± 0.026) in the Canadian portion of our study area (Hovey and McLellan 1996). The density of grizzly bears in our study area is greater than any other area of North America except coastal Alaska (McLellan and Hovey 1995). Bears primarily affect cervid populations by their impact on neonates (see citations below) but they also have been shown to be efficient predators on adult moose and caribou (Boertje et al. 1988, Bangs et al. 1989, Larsen et al. 1989). Based on scats, cervids (primarily elk) and roots dominate the diet of grizzly bears in our study area during April and early May and again in late September and October (McLellan and Hovey 1995). Based on the sample of radio-tagged cervids, we found mortality caused by bears to be highest from May-August. Cervids showing up in scats during spring may be from scavenging and not predation alone. Also, scat analysis may underestimate the importance of cervids in bear diets due to the small amount of hair ingestion by bears. We examined mortality rates in only female cervids (primarily adults), but fawns/calves or males may be more vulnerable to bears in late spring. Similar to results from our study, McLellan and Hovey (1995) found much yearly variation in the presence of cervids in grizzly bear diets. Availability of other foods probably affects the variation (McLellan and Hovey 1995).

Given the increasing populations of bears, wolves, and cougars and their high densities in our study area, it is not surprising that deer and elk populations declined. Had there been more winters of average or above average severity, the decline probably would have been more precipitous. The high cervid:predator ratio also probably slowed the declines. The present cervid:predator ratio warrants special vigilance by wildlife managers to avoid prolonged low cervid densities. Low prey densities reduce hunter opportunities and as a result may reduce tolerance for large carnivores by some portions of the public. Additionally, low prey densities may slow recovery of endangered wolves and potentially even threatened grizzly bears (McLellan and Hovey 1995).

The correlation between wolf numbers and cervid population declines is clear, but the mechanism for the declines is less clear. Adult survival rates are similar to rates in other areas where populations are stable or increasing. A major factor driving these declines is the low recruitment rates. The spring elk cow:calf (100:11-16) and doe:fawn ratios (100:25-39) in the NF are very low when compared to other areas (elk: 100:21, Schwartz and Mitchell 1945; 100:24, Knight 1970; 100:25, 100:48, Demarchi and Wolterson 1991; Schlegel 1976; 100:22 [mean late winter ratio 1986-1991], Coughenour and Singer 1996; deer: 100:42, Nelson and Mech 1981; 100:51, Sime 1995). Recruitment rates (R; calculated using method of Hatter and Janz 1994) in the NF (R = 0.13) were similar to recruitment rates during the 7 year deer decline on Vancouver Island (R = 0.09; Hatter and Janz 1994). Population change there was more sensitive to recruitment than to adult survival rates (Hatter and Janz 1994, but see Nelson and Peek 1982, Fuller 1990). To achieve a stable population trend for deer in the NF (λ = 1.00) given the current adult female survival rates, a fawn:doe ratio of 100:70 would be required. Alternately, an adult female survival rate of 0.87 would be required to achieve the same objective given the current recruitment rate.

The majority of elk calf mortality probably occurs in the summer because most of the decline in cow:calf ratios occurred by August (Bureau 1992) and we found very few calves killed in the winter while backtracking wolves (chapter 1). The timing of mortality is less clear for deer fawns. Factors responsible for the high mortality are unknown. Numerous studies during the past 15 years in Canada and Alaska have concluded that wolves and bears are important predators on newborns and thereby limit growth of moose and caribou herds (Schlegel 1976, Franzmann et al. 1980, Gasaway et al. 1983, Keith 1983, Messier and Crete 1985, Gasaway et al. 1986, Bergerud and Ballard 1988, Larsen et al. 1989). Cougars and coyotes may also be significant predators on neonates and young fawns. Bergerud (1988) believed that because recruitment of calves and mortality of adults were negatively correlated (similar to our study) in 17 herds of caribou in North America, a common mortality factor (predation) was responsible. Even so, we cannot rule out factors other than predation in the low recruitment rates and resulting population declines.

Multi-prey, Multi-predator Effects

Little information exists on the effects of multiple predators and multiple prey on large mammal predator-prey dynamics. The effect of an additional predator has only been examined in detail in moose-wolf systems. Messier and Crete (1985), Crete (1987), Van Ballenberghe (1987), Gasaway et al. (1992), and Messier (1994) believed that a second predator, particularly one in which predation is believed to be density independent, would produce a low-density equilibrium of moose. Moose can be confined to low-density fluctuations for long periods of time when bears and wolves are present (Van Ballenberghe and Ballard 1994); the conditions leading to this situation are unclear. The effects of more than one predator on other cervid systems are almost wholly unknown as is the effect of 3 large predators on any cervid system.

Predation by multiple predators in the North Fork was largely additive. Additive effects fall along a continuum (F. Messier, Univ. Saskatchewan, pers. comm.). We acknowledge that any animal killed by one predator is not available to another predator, and that the death of one deer "frees" up resources for another deer. Wolf and cougar predation rates on deer were not correlated. Both wolves and cougars readily took prime-aged deer and deer that, based on FMF content, probably would have survived the winter had they not been killed by predators. This assumption is tenuous based on the fact that some kills occurred early in winter and FMF levels may dip below thresholds by winter's end. Additionally, other stressors may result in the death of an animal even if FMF value is above the threshold (Mech et al. 1995).

Mortality agents have generally been found to be additive when cervid populations are below carrying capacity (Gasaway et al. 1983, Ballard and Larsen 1987, Gauthier and Theberge 1987, Gasaway et al. 1992). Potvin et al. (1988) found that low deer densities in Quebec were not followed by a similar decline in the wolf density because wolves switched to killing primarily prime-aged deer in good condition. Alternately, McCullough (1984) argued that when the proportion of the deer population (at or near carrying capacity) taken by hunters is increased, deer condition improves and the proportion taken by other predators should decrease. Filonov (1980) found a high degree of substitution among mortality factors acting on moose, red deer, sika deer (Cervus nippon), roe deer (Capreolus capreolus), and reindeer (Rangifer tarandus) on reserves in the former Soviet Union. Despite this conclusion, she reported that mortality of ungulates was highest during years of high wolf density. Additionally, much of the compensatory response she observed occurred when prey was probably at or above carrying capacity. Human-caused mortality (hunting) was found to be additive to other mortality in adult female white-tailed deer in 3 areas of Montana (Dusek et al. 1992). These authors believed that manipulation of the fawn segment of deer populations "offers the only opportunity for implementing compensation theory in deer management" (Dusek et al. 1992:649).

The deer population in our study area appeared to be below carrying capacity based on diastema trends and comparisons to other areas in northwestern Montana (Reimers 1972, Frisina and Douglass 1989). The diastema evidence is less certain for elk. However, the current low density of elk combined with the favorable habitat created by recent fires and the lack of obvious signs of "overuse" of their winter range (K. Kunkel, pers. obs.) point to an elk population below carrying capacity. We traveled over 700 km throughout the study area from 1992-1996 and only found 8 winter-killed elk and deer. We recognize that starvation levels do not necessarily indicate that animals are not in danger of starvation; to avoid predation, animals may increase their probability of predation (McNamara and Houston 1987).

Little is known about how alternate prey affect cervid-wolf systems (Messier 1994). Two outcomes may be possible: alternate prey may either dilute or exacerbate the effects of the predator on the primary prey. Dilution (by diversion) might be expected where alternate prey is more vulnerable [(Pimlott et al. 1969, Carbyn 1983, Potvin 1988) cited in Messier 1994]. Exacerbation might be expected where the alternate prey produces a numerical response in the predator. These are probably not mutually exclusive.

Bergerud and Elliot (1986) believed that increases in moose density supported increases in wolf density and because wolves preferentially preyed on caribou, this resulted in declines in caribou density. Coastal caribou populations with few alternate prey support higher caribou densities than interior populations with moose present (Valkenburg et al. 1996 cited in Boertje et al. 1996). Fuller (1990) believed the impact of wolves on deer in northeastern Minnesota was exacerbated by the abundance of moose. Tests of these competing theories have not been conducted. The dilution theory seems most plausible within our study area, at least over the short term, where deer and moose coexist. Where deer were present in our study area, the wolf-caused mortality rate on moose was significantly lower than in areas where deer were absent. The presence of deer on moose summer ranges in our study area may have diverted wolf predation from moose and allowed moose numbers to increase despite the presence of 3 species of predators. Densities of moose in our study area (0.42-0.55/km^2; Langley 1992) are higher than the mean density of moose in areas in Alaska and Yukon where wolves and bears are only lightly harvested (0.15/km^2; Gasaway et al. 1992) but they are not as high as densities in other systems where ungulates assumed more vulnerable than moose are also found (0.6-1.3 km^2; Bergerud 1992). The moose density in our study area is at the upper end of the range that Messier (1994) referred to as low-density equilibrium where predation may regulate numbers.

We could not compare mortality rates of deer or elk in the presence and absence of each other because there was no portion of our study area where spatial separation occurred, however, we did find a correlation between the decline of elk in our study area and an increase in selection of deer by wolves (chapter 4). This may in the long term exacerbate the decline in elk numbers because the presence of deer may maintain wolf numbers and predation pressure on elk.

CONCLUSIONS

Our results generally supported the hypotheses that deer and elk populations are in decline and that predation is the primary limiting factor.

MANAGEMENT IMPLICATIONS

Significant declines in local cervid populations that might occur as wolf recolonization continues in the Rocky Mountains will be unpopular with local people (Tucker and Pletscher 1989). Declines will result in low cervid:wolf ratios, a situation where the impact of wolves and other predators is most significant. Once this situation arises, cervids may be maintained at low equilibrium for extended periods yielding lower harvests and ultimately lower predator densities (Boertje et al. 1996). Managers must be especially alert to changes in cervid population trends and the causes for these trends. Increased monitoring efforts will be required in areas where wolf recovery is occurring, especially in those areas where cougars and bears are also present. Managers should expect lower cervid populations that may remain low for extended periods where all 3 predators are present. Managers should also inform the public about this possibility. Because wolf reductions will probably not be an option in the immediate future as a response to cervid declines, managers must be prepared to reduce hunting pressure (Gasaway et al. 1983, Fuller 1990). Managers have the option to increase harvest pressure on other predators to enhance prey populations (Boertje et al. 1995). Habitat improvement and manipulation of alternate prey may also benefit prey populations (Boettje et al. 1995, chapter 3). Enhancement of white-tailed deer populations may divert predation pressure on moose and reduction of white-tailed deer populations may reduce wolf density and predation levels on elk, although more research is necessary to substantiate this.

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CHAPTER 3: HABITAT FACTORS AFFECTING SUCCESS OF WOLVES AND COUGARS HUNTING WHITE-TAILED DEER IN NORTHWESTERN MONTANA

Abstract: We examined factors affecting hunting success of wolves (Canis lupus) and cougars (Puma concolor) in a multi-prey system in northwestern Montana. Wolves concentrated their hunting during winter in white-tailed deer (Odocoileus virginianus) yards and selected against encounters with elk (Cervus elaphus). They used areas where travel was easiest and habitats that were favored by white-tailed deer. Wolves killed deer in areas with higher densities of deer and lower densities of elk and moose than were available along wolf travel routes. They killed deer in areas with greater hiding/stalking cover and less slope than was available on wolf travel routes. More deer were killed by wolves at non-vegetated sites (ice) and in young trees and in the upland spruce (Picea spp.) cover type than was available along travel routes. Fewer deer were killed in the sapling size class, burned cover type, and in the lodgepole pine (Pinus contorta) cover type and more deer were killed in the main valley bottom, in ravines, and at sites closer to water than was available along travel routes. Compared to control sites, more deer were killed by wolves at flatter sites and at sites with lower densities of deer. Cougars killed deer at sites with greater slope, more mature trees, and greater canopy coverage than was present at sites where wolves

killed deer. Cougar kill sites were closer to water than wolf kill sites. Cougar kill sites had lower densities of deer and were further from deer trails than control sites. Antipredator strategies used by deer to avoid wolves may not be as successful for avoiding cougars and vice versa. Managers interested in reducing vulnerability of deer to wolf and cougar predation should maximize deer density in a few large yards and should thin stalking cover in those yards. Habitat fragmentation and roads should be minimized to reduce wolf search and travel efficiency.

INTRODUCTION

The killing rate of a predator is a product of 3 factors: 1) the rate of prey encounter, 2) the rate of prey detection, and 3) the probability of a successful capture of an individual once it is detected (Taylor 1984). Most research on predator-prey relationships in large mammals has focused on the third factor by examining how animal condition affects vulnerability of prey to capture. Condition of animals is not the only factor affecting probability of successful capture. We know that predators, including wolves and cougars, do not kill only animals in poorer condition (Kenward 1978, Temple 1987, Potvin et al. 1988, chapter 1 and 2), suggesting that factors 1 and 2 may be equally or more important in determining capture success. In fact, animal condition may be only a minor factor for predators that rely on stealthy approach and ambush to capture prey (Schaller 1972, Kruuk 1972). Habitat features and spatial relationships between predators and prey may affect selection and vulnerability of prey and weigh heavily in capture success (Bergerud et al. 1983, Stephens and Peterson 1984, Van Ballenberghe 1987, Bergerud and Snider 1988).

Pimlott (1967), Mech (1970), Keith (1974), and Boertje et al. (1996) suggested that predation may, at times, be the primary factor limiting numbers of ungulates. Van Ballenberghe (1987) suggested that the question is no longer whether predation is limiting, but rather under what conditions prey declines occur and how long such conditions last (cf. Sinclair 1991 and Boutin 1992). Spatial relationships between predators and prey and habitat features may be important components in setting these conditions. Tanner (1975) modelled several predator-prey systems, including some with 5 species of ungulates, and reported that long search time flattened the rise in predator kill rates and thereby contributed stability to predator-prey interactions. Populations with widely-spaced individuals may support higher ungulate numbers as may areas with ample escape habitat. Both of those conditions increase the searching time required of wolves. Bergerud and Snider (1988) hypothesized that the spacing of predator and prey determines the predation rate and sets equilibrium density of prey below that dictated by food.

Van Ballenberghe (1987), Lima and Dill (1990), and Skogland (1991) and other researchers working on a wide variety of predator-prey systems indicated that spatial features, including environmental heterogeneity, significantly affect the ability of predators to encounter and kill prey. Certain types of habitat patches may provide refuges that reduce detection and capture of prey (Wolff 1981, Skogland 1991, Crawley 1992). Similarly, certain habitats may allow prey to detect predators before the predators are within killing distance (Elliot et al. 1977, Van Orsdal 1984). Elements of habitat structure and physiographic features may allow prey to successfully evade predators. Miller (1975) reported that wolf-killed caribou (Rangifer tarandus) were not randomly distributed and that certain sites must provide wolves with an advantage over their prey. Peterson and Woolington (1981) found that most wolf-killed moose on the Kenai Peninsula, Alaska were in small stands of timber remaining in old burns. Stephens and Peterson (1984) suggested that moose seek conifer cover and its associated structure to reduce attack rates by wolves.

Knowledge of how habitat and spatial factors affect vulnerability of prey may suggest how wildlife managers can manage habitats and landscapes to affect predation rates to meet objectives for populations of predators and prey. Recent work on the role of habitat and spatial factors in relation to vulnerability of elk to hunters has provided several management applications (Christensen et al. 1991, Unsworth et al. 1993, Weber 1996).

As wolves recolonize the western U.S., they will become an important mortality factor on ungulate populations and may at times be the primary limiting factor (chapter 2). For social and political reasons, control of wolf populations that limit ungulate populations below desired levels will not be an option in the near future, and may never be (Boertje et al. 1995, Mech 1995). For this reason, we need to examine alternative ways of altering wolf/ungulate dynamics (Boertje et al. 1995). Manipulating habitat and spatial factors may be one way of achieving wolf and ungulate population objectives. We examine other alternatives elsewhere (chapters 1, 2, and 5).

We examined predator-prey relationships between wolves (Canis lupus), cougars (Puma concolor), white-tailed deer (Odocoileus virginianus), elk (Cervus elaphus), and moose (Alces alces) in the North Fork of the Flathead Valley in Montana from 1990 through 1996. Our objective was to determine the effects of spatial and habitat features on hunting success (and thereby vulnerability of prey) of wolves and cougars.

METHODS

Field Methods

Wolves were captured, sedated, and radiocollared following techniques described by Mech (1974) and Ream et al. (1991). Wolves were located from the ground or the air > 4 times/week during winter (Nov-Apr) to locate their travel routes. Travel routes were found by bisecting the area between consecutive daily locations of wolves. We followed these routes forward and backward on skis, snowshoes, or on foot to locate kills and estimate habitat and spatial variables deemed important to where wolves hunted and made kills. We did not work in areas where we knew wolves were present to minimize our effects on wolf behavior.

Hornocker Wildlife Institute personnel captured cougars using hounds released on cougar tracks (Murphy et al. 1992, Ruth et al. 1995) and then immobilized and radiocollared them (Hornocker and Wiles 1972). They located cougars daily from the ground and weekly from the air. They found kills made by cougars by snow-tracking radiocollared cougars and by following cougar tracks during capture efforts. Cougar kills were also located while following travel routes of wolves.

White-tailed deer (deer) were captured in traps (Clover 1956). Females were fitted with radio transmitters containing mortality sensors and were monitored for mortality signals 2-3 times/week during winter and spring and 1-2 times/week during summer and fall. When a mortality signal was received, the collar was located and the site and any remains were examined to determine cause of death. Mortality signals of radiocollared animals were usually investigated 1-4 days after death.

For all kills, predation was considered to be the cause of death when blood, subcutaneous hemorrhaging at wound sites, or sign of a struggle was found at the site. Evidence such as cougar or wolf hair, tracks, scats, presence of buried carcass, plucked hair, kill and feeding pattern, and percent of carcass found was used to classify the predator responsible for death (O'Gara 1978, chapter 1).

The location of the carcass was considered to be the kill site unless track or other site evidence indicated otherwise. Habitat variables were measured in a 30 m radius plot centered on the kill site. Percent canopy coverage was estimated using 2 methods. First, canopy over the plot was compared to schematic drawings presented in Unsworth et al. (1991) and placed into 1 of 5 categories: 1) 0-10%, 2) 11-30%, 3) 31-50%, 4) 51-75%, and 5) 76-100% (1993 method). Second, canopy was estimated by counting the number of points under canopy cover at 2-m intervals along 2 (1 N-S, 1 E-W) 20 m perpendicular transects centered on the carcass, and then placed into one of the 5 categories (1994-95 method). Percent hiding cover category was determined by visually estimating the percent of a deer obscured at 30 m in the 4 cardinal directions from the carcass. Hiding cover was divided into the same 5 categories as canopy coverage.

The mean of the cover classes from the 4 directions was considered to be the hiding cover for the site. In 1993, only an overall estimate for the plot was made and placed into one of the 5 categories. J. Lyon (USDA Forest Serv., pers. commun.) found these techniques yielded results that were the same as those obtained using cover boards. At the start of each field season, all project personnel spent a day in the field standardizing hiding cover classifications.

Vegetation cover type at the site was classified based on the types developed by Jenkins and Wright (1988; Table 1). We added several more cover types for sites occurring outside the floodplain examined by Jenkins and Wright (1988) and combined some similar types. Structural class of the dominant vegetation at the site was placed into one of 8 categories (Table 2). We recorded whether a structural class different from that of the plot could be seen. The number of downed logs (> 4 cm diameter) that had to be stepped over while walking 10 m N from plot center was recorded. The mean height of these logs was determined by measuring the distance from the ground to the top of each log.

Five snow depths were measured, each at 2 m intervals on a transect going N from plot center. If present, 5 prey track depths and 5 predator track depths (wolf or cougar)

Table 1. Cover types at wolf kills, control sites, wolf routes, and systematic routes in and near Glacier National Park, Montana for winter 1993-1996.

Type	Proportion of occurrence wolf kills	Proportion of occurrence at control site	Proportion of occurrence on wolf route[a]
Open/shrub	0.10 (11)	0.09 (8)	0.12 (106)
Ice	0.11 (13)[bc]	0.09 (8)	0.02 (17)[b]
Burnt timber	0.04 (5)[d]	0.05 (5)	0.16 (138)[de]
Deciduous	0.03 (3)	0.03 (3)	0.04 (38)[f]
Larch/Ponderosa	0.04 (5)	0.04 (4)	0.04 (34)
Douglas Fir	0.16 (18)	0.20 (19)	0.07 (62)
Lodgepole	0.05 (6)[g]	0.07 (6)	0.13 (117)[gh]
Upland spruce	0.35 (40)[i]	0.27 (25)	0.21 (188)[i]
Lowland conifer	0.12 (14)	0.16 (15)	0.21 (185)[j]
	systematic[k]	cougar kill[l]	cougar control
Open/shrub	0.09 (44)	0.07 (6)	0.06 (2)
Ice	0.00 (2)	0.00 (0)[c]	0.03 (1)
Burnt timber	0.09 (45)[c]	0.02 (2)	0.06 (2)
Deciduous	0.10 (52)[f]	0.06 (5)	0.00 (0)
Larch/Ponderosa	0.07 (34)	0.07 (6)	0.03 (1)
Douglas Fir	0.07 (37)	0.27 (22)	0.31 (11)
Lodgepole	0.22 (114)[h]	0.11 (9)	0.17 (6)
Upland spruce	0.25 (129)	0.26 (21)	0.20 (7)
Lowland conifer	0.10 (55)[j]	0.13 (11)	0.14 (5)

Table 1. Continued

[a] Significant difference ($\chi^2 = 57.65$, 8 df, $\underline{P} < 0.00001$) between wolf kill and wolf route

[b] $\underline{P} < 0.0001$

[c] $\underline{P} = 0.02$

[d] $\underline{P} = 0.10$

[e] $\underline{P} = 0.004$

[f] $\underline{P} < 0.0001$

[g] $\underline{P} = 0.10$

[h] $\underline{P} < 0.0001$

[i] $\underline{P} = 0.009$

[j] $\underline{P} < 0.0001$

[k] Significant difference ($\chi 2 = 80.82$, 8 df, $\underline{P} < 0.00001$) between wolf route and systematic route

[l] Significant difference ($\chi^2 = 17.93$, 8 df, $\underline{P} = 0.02$) between wolf kill and cougar kill

Table 2 Structural class of wolf kills, control sites, wolf routes, and systematic routes in and near Glacier National Park, Montana for winter 1993-1996.

Class	Proportion of occurrence wolf kills	Proportion of occurrence at control site	Proportion of occurrence on wolf route[a]
Non-vegetated	0.12 (13)[bc]	0.08 (7)	0.01 (4)[b]
Herbaceous	0.08 (9)	0.02 (2)	0.09 (34)
Shrub/seedling	0.03 (3)	0.08 (7)	0.05 (20)
Sapling	0.01 (1)	0.00 (0)	0.03 (12)
Pole/sapling	0.05 (6)[d]	0.07 (6)	0.18 (71)[d]
Young trees	0.45 (50)[e]	0.41 (34)	0.28 (113)[e]
Mature trees	0.26 (29)[f]	0.33 (27)	0.34 (137)
	systematic[g]	cougar kill[h]	cougar control
Non-vegetated	0.01 (1)	0.00 (0)[c]	0.03 (1)
Herbaceous	0.02 (2)	0.03 (2)	0.09 (3)
Shrub/seedling	0.02 (2)	0.09 (7)	0.06 (2)
Sapling	0.02 (2)	0.01 (1)	0.06 (2)
Pole/sapling	0.14 (15)	0.06 (5)	0.09 (3)
Young trees	0.35 (36)	0.37 (30)	0.46 (15)
Mature trees	0.44 (46)	0.44 (36)[f]	0.21 (7)

[a] Significant difference ($\chi^2 = 50.05$, 6 df, $\underline{P} < 0.00001$) between wolf kill and wolf route

[b] $\underline{P} < 0.0001$

[c] $\underline{P} = 0.01$

[d] $\underline{P} = 0.01$

[e] $\underline{P} = 0.007$

[f] $\underline{P} = 0.06$

Table 2. Continued

[g] Significant difference ($\chi^2 = 10.9$, 6 df, $\underline{P} = 0.092$) between wolf route and systematic route

[h] Significant difference ($\chi^2 = 19.39$, 4 df, $\underline{P} = 0.001$) between wolf kill and cougar kill

were measured within the plot. Slope at each plot was estimated using a clinometer and aspect was recorded to the nearest degree. Topographic position (U.S. Forest Serv. ecodata; Table 3) of each plot was also recorded.

To estimate relative densities of prey at the sites, we skied 2 100 m transects in opposite directions starting at plot center. At kill sites, we attempted to place these transects perpendicular to the travel route of the predator responsible for the kill. If the travel route was not known, and if the site was on an incline, the transects were oriented up and down the slope. If neither of these conditions applied, the transects went east and west. The distance to the first deer, elk, and moose track on each transect was recorded. If no track was encountered the distance recorded was 100 m. The number of deer, elk, and moose tracks located on both transects (0, 1, or 2; only the first track on each transect was recorded) was divided by the distance to that track (e.g. 1/190 if one deer track was found at 90 m in one direction and no deer track was found along the opposite 100 m transect) to obtain the number of deer, elk, and moose tracks/m. This value was divided by the number of days since the most recent snowfall of > 5 cm to adjust for snowfall effects. We set seven as the maximum number of days since snowfall because after this track deposition had plateaued and tracks started to deteriorate (K. Kunkel, pers. obs.). Tracks were classified as either:

Table 3. Topographic class of wolf kills, control sites, wolf routes, and systematic routes in and near Glacier National Park, Montana for winter 1993-1996.

Class	Proportion of occurrence wolf kills	Proportion of occurrence at control site	Proportion of occurrence on wolf route[a]
Valley bottom[1]	0.27 (30)[b]	0.29 (24)	0.15 (60)[b]
Ravine	0.08 (9)[c]	0.04 (3)	0.01 (4)[c]
Lower slope[2]	0.07 (8)[d]	0.18 (15)	0.15 (58)[e]
Mid/up slope[2]	0.05 (5)	0.07 (6)	0.10 (38)
Wide valley slp	0.24 (26)	0.17 (14)	0.32 (128)[f]
Ridgetop/knoll	0.06 (6)	0.04 (3)	0.06 (23)
Bench/terrace	0.16 (17)	0.18 (15)	0.15 (58)
Creek bottom	0.08 (9)	0.05 (4)	0.06 (22)[g]
	systematic[h]	cougar kill[i]	cougar control
Valley bottom	0.11 (10)	0.24 (19)	0.18 (6)
Ravine	0.01 (1)	0.04 (3)	0.03 (1)
Lower slope	0.33 (31)[e]	0.27 (22)[d]	0.38 (13)
Mid/upper slope	0.11 (10)	0.07 (6)	0.09 (3)
Wide valley slp	0.05 (5)[f]	0.16 (13)	0.06 (2)
Ridgetop/knoll	0.02 (2)	0.01 (1)	0.03 (1)
Bench/terrace	0.19 (18)[g]	0.14 (11)	0.18 (6)
Creek bottom	0.19 (18)	0.07 (6)	0.06 (2)

Table 3. Continued

[1] Main valley
[2] Side valley
[a] Significant difference ($\chi^2 = 33.42$, 7 df, $\underline{P} = 0.00002$) between wolf kill and wolf route
[b] $\underline{P} = 0.03$
[c] $\underline{P} = 0.001$
[d] $\underline{P} = 0.003$
[e] $\underline{P} = 0.0008$
[f] $\underline{P} < 0.0001$
[g] $\underline{P} = 0.005$
[h] Significant difference ($\chi^2 = 33.65$, 7 df, $\underline{P} = 0.00002$) between wolf route and systematic route
[i] Significant difference ($\chi^2 = 17.89$, 7 df, $\underline{P} = 0.012$) between wolf kill and cougar kill

1) single animal, 2) light trail (2-3 animals), 3) medium trail (4-6 animals) or 4) heavy trail (packed trail or runway). The distance to a cervid trail (medium or heavy trail) was tabulated the same way as distance to the first track.

Spatial Analysis

Universal transverse mercator (UTM) coordinates from a 1:24,000 scale map or from a global positioning system receiver were recorded at each habitat plot. These coordinates were entered into a geographic information system (PAMAP GIS, ARCINFO). Spatial and vegetative attributes were generated for each site from GIS map layers of the study area created by Singleton (1995) and the Montana Cooperative Wildlife Research Unit Spatial Analysis Laboratory (Redmond 1996). These included maps representing cover type, size class, canopy coverage, modified normalized difference vegetation index (a measure of absorption variation in middle infrared wavelengths which are known to be associated with canopy closure; Butera 1986, Redmond 1996), topographic position, slope, aspect, distance to open roads, distance to trails, and distance to water. A new variable called "travdis" was created to measure the distance to a linear feature that could be used by wolves for travel; this was the shortest of the distance to roads, distance to trails, or distance to water. We created cover type and size class polygons from which we could estimate area of the polygon and distance to edge of the polygon.

Scales of Analysis

All of the above mentioned variables were also recorded at non-kill sites for later comparison with kill sites. Because factors affecting vulnerability of prey and hunting strategies of wolves probably occur at different scales, comparisons were made at 3 different scales. At the wolf home range scale (prey encounter level), we skied track transects at 1 km intervals and measured habitat variables at sites spaced 3 km apart along systematic transects that followed hiking trails, roads, and pellet transects (chapter 1; Fig. 2, chpt. 1). These variables were compared to variables collected at 1 km intervals along wolf travel routes to test the null hypothesis that habitat and spatial variables where wolves chose to travel and hunt did not differ from what was available in their home range.

At the next finer scale of analysis, we tested the null hypothesis that habitat and spatial variables did not differ between sites along wolf hunting routes and sites where wolves killed deer. At the finest scale of comparison, we tested the null hypothesis that habitat and spatial variables at kill sites did not differ from the same variables measured at "control" sites which were 500 m in a random direction from wolf kill sites.

To compare factors affecting wolf and cougar hunting success and thus affecting deer vulnerability to these 2 predators, habitat and spatial variables at wolf kill sites were compared to those at cougar kill sites. We also tested the null hypothesis that habitat and spatial variables at cougar kill sites did not differ from the those measured at "control" sites which were 500 m in a random direction from cougar kill sites.

Statistical Analysis

We used univariate analyses to test the null hypothesis that individual variables did not differ between paired site class comparisons (e.g. wolf kill sites vs. control sites). Because we were testing different hypotheses with each comparison of site pairs, no adjustments of $\underline{P}$ values were deemed necessary for these tests (Rice 1989). None of the interval scale variables were judged normal based on the Lilliefors test (Norusis 1993) and no transformations successfully normalized them, so we used Kruskall-Wallis (KW) tests to compare these variables among sites. When large sample size was the suspected reason for rejection of the normality assumption, we also examined results of 2-sample $\underline{t}$ tests. When the KW test was significant ($\underline{P} < 0.10$), we compared pairs of sites using Mann-Whitney $\underline{U}$ statistics.

Snow depths were compared between sites by pairing sites examined on the same day. Because snow depths were not normally distributed but were symmetrical we used the Wilcoxen Matched Pairs test to make comparisons. Categorical habitat variables were cross-tabulated by pairs of sites (e.g. travel vs kill sites). We used Pearson's Chi-square statistic to test the null hypotheses of independence among categories. When > than 20% of cells had expected values < 5, we combined adjacent (similar) categories. We rejected null hypotheses when $\underline{P} \leq 0.05$. Adjusted standardized residuals ([observed - expected/expected$^{0.5}$]/standard error) were used to identify significant cells (Habermann 1973). Probability values were adjusted by multiplying by the number of cell pairs in the cross-tabulation (Bonferroni adjustment-e.g. overall $\underline{P}$ = 0.001 and cell pairs = 5 , 0.001*5 = 0.005; Rice 1989).

Stepwise logistic regression (Norusis 1993, Trexler and Travis 1993) was used to predict the probability of successfully classifying pairs of sites (dependent variable) using habitat and spatial variables for prediction. Five models with the following dichotomous dependent variables were examined: 1) systematic route or wolf travel route, 2) wolf travel route or kill site, 3) wolf kill site or control site, 4) wolf kill site or cougar kill site, and 5) cougar kill site or control site. Independent variables included were those that were found to be significant in the univariate tests (Capen et al. 1986). Snow depth variables were not included because they had to be paired by date for analysis. Including them would have significantly reduced the sample size that could be used in the logistic regression analysis. Correlation analysis was conducted on all the independent variables used in the regression models and the least explanatory of highly intercorrelated variables was removed during model building to reduce the likelihood of inaccurate results resulting from multicollinearity (Trexler and Travis 1993). Independent variables were entered into the model at the 0.10 significance level and removed at the 0.11 level using the likelihood-ratio test (Norusis 1993). The Wald statistic was used to test whether the coefficient of individual classes of categorical variables was different from zero. Regressions were run separately for 1993 and 1994-1996 data due to some differences in methodology between years (see above) and after univariate tests revealed difference in these variables between these years. Final models were assessed for reliability using goodness-of-fit maximum likelihood estimates, accuracy of classification tables, estimates of $\underline{R}^{2logit}$ (Hair et al. 1995), and significance tests of coefficients (Norusis 1993, Trexler and Travis 1993). Initial overall prediction success values for classification tables resulted from predicting that all observations fell into one of the 2 site classes. For example, if 100 cougar kill sites and 200 wolf kill sites were examined, all 300 of these sites would be predicted to be wolf kill sites in the initial classification table. This would yield an overall prediction success of 67% (200/300) since all of the wolf kill sites would have been classified correctly and all of the cougar kill sites would have been classified incorrectly.

RESULTS

Wolf Hunting Area Selection

Wolves selected areas for hunting that had lower snow depths (med = 23.5 cm, n = 91 vs 31.5 cm, n = 81; Mann-Whitney [MW] Z = -2.30, P = 0.021) and marginally shallower deer track depths (med = 13.5 cm, n = 54 vs 16.0 cm, n = 70; MW Z = -1.75, P = 0.081) than were found along systematic routes.

Wolves selected areas for hunting with fewer elk (MW Z = -2.23, P = 0.026), less hiding cover (MW Z = - 5.30, P < 0.00001) and a greater degree of slope (Mann-Whitney [MW] Z = -1.90, P = 0.05; Table 4) than was available within their home range. They used lower slopes in side valley bottoms and creek bottoms less and wide valley slopes more (Table 3). They used burnt timber and lowland spruce cover types more and deciduous and lodgepole pine cover types less (Table 1). Wolves hunted in areas with a lower modified normalized difference vegetation index (NDVI; MW Z = -1.87, P = 0.06; Table 4) and closer to the edge of size class

Table 4. Habitat and spatial variables associated with various sites in and near Glacier National Park, Montana, 1993-1996.

site	deer track/km		elk track/km		moose track/km		aspect		deadfall		hiding cover	
	$\bar{x}$	med	$\bar{x}$	med	$\bar{x}$	med	$\bar{x}$	med	$\bar{x}$	med	$\bar{x}$	med
Wolf kill	32.9	7.0	0.3	0.0	0.2	0.0	134.7	135.0	28.3	25.0	12.8	13.0
	18.0[1]	101[2]	0.0	102	0.0	102	14.7	61	4.4	54	0.7	62
Wolf kill control	38.7	11.0	2.3	0.0	0.2	0.0	122.3	148.0	30.0	32.0	12.3	13.0
	8.0	81	0.0	81	0.0	81	14.0	49	3.7	46	0.7	50
Wolf travel	21.7	2.0	2.4	0.0	1.1	0.0	151.3	180.0	19.4	18.0	10.4	10.0
	1.0	932	0.0	933	0.0	933	5.7	386	2.8	47	0.2	387
Systematic	12.4	1.0	2.6	0.0	1.4	0.0	144.0	135.0	27.2	27.0	13.4	14.0
	2.0	696	1.0	696	0.0	696	11.3	92	2.7	95	0.5	95
Cougar kill	29.6	7.0	0.0	0.0	0.0	0.0	136.9	145.0	20.9	19.0	13.0	13.0
	7.0	74	0.0	70	0.0	70	14.8	55	3.0	54	0.6	57
Cougar control	43.5	31.0	0.0	0.0	0.0	0.0	144.6	160.0	26.5	21.0	12.5	12.0
	8.0	32	0.0	32	0.0	32	18.6	21	4.8	19	1.3	21

Table 4. Continued

site	slope		trail distance		NDVI[3]		SC edgedis[4]		SC area[5]	
	$\bar{x}$	med	$\bar{x}$	med	$\bar{x}$	med	$\bar{x}$	med	$\bar{x}$	med
Wolf kill	5.4	2.0	167.7	200.0	6629.8	401.0	666.5	508.0	3628.9	4355.0
	0.9	84	9.5	27	1731.0	115	52.0	115	339.1	115
Wolf kill control	9.7	5.0	139.7	168.0	6001.3	414.5	585.0	364.0	3404.9	1713.0
	1.6	61	14.1	24	1910.6	90	55.9	90	376.5	90
Wolf travel	8.5	7.0	155.0	200.0	2369.5	344.0	668.8	435.0	3959.4	4355.0
	1.1	50	3.3	364	575.0	369.0	37.4	369	196.3	369
Systematic	5.9	3.0	na	na	3455.0	352.0	1061.9	687.0	4572.9	4355.0
	0.8	95	na	na	1207.7	111	110.5	111	370.2	111
Cougar kill	8.1	4.5	149.3	162.5	2267.3	400.5	543.2	212.0	4088.1	4355.0
	1.1	68	11.7	22	1223.3	74	76.2	74	482.3	74
Cougar control	10.7	8.0	110.6	102.0	4142.7	408.0	549.1	423.5	4722.0	4630.0
	2.2	26	16.5	13	2625.4	34	82.8	34	706.0	34

Table 4. Continued

site	travdis[6]		road distance		trail distance		stream distance	
	x̄	med	x̄	med	x̄	med	x̄	med
Wolf kill	227.8	125.0	1657.5	849.5	1465.3	1304.0	348.5	175.0
	23.9	115	122.9	371	103.7	116	32.9	116
Wolf kill control	238.6	121.0	1952.2	886.0	1359.4	1156.5	339.9	184.5
	29.6	90	255.7	90	113.3	90	38.4	90
Wolf travel	283.0	207.0	1719.7	740.0	1645.3	1386.0	386.5	290.0
	14.7	369	122.9	371	66.1	371	17.8	371
Systematic	na	na	na	na	na	na	na	na
Cougar kill	166.3	75.0	2585.0	875.0	1211.1	866.0	271.6	152.5
	30.6	74	349.1	76	138.5	76	39.5	76
Cougar control	196.1	140.5	2816.4	581.5	1298.2	1193.0	266.7	205.0
	31.8	34	576.1	34	156.3	34	35.3	34

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[1] SD

[2] n

[3] normalized difference vegetation index (Nemani et al. 1993)

[4] distance to edge of size class polygon

[5] area of size class polygon

[6] distance to closest road, trail, or stream

polygons (MW $\underline{Z} = -2.50$, $\underline{P} = 0.012$; Table 4).

During 1993 wolves selected areas for hunting with more deer (med = 0.0 vs 0.0, MW $\underline{Z} = -3.15$; $\underline{P} = 0.0017$) and elk (med = 4.0 vs 3.0, MW $\underline{Z} = -4.70$; $\underline{P} < 0.0001$) and less moose (med = 1.2 vs 0, MW $\underline{Z} = -4.61$, $\underline{P} < 0.00001$) than was available along systematic routes.

Logistic regression.--

The simplest multivariable model that predicted (χ^2 = 138.18, 13 df, $\underline{P} < 0.00001$) the probability that a specific location in wolf home ranges would be used as a wolf hunting routes ($\underline{h}$) used slope, position, NDVI, hiding cover, distance to edge of size class, canopy, and cover type (Table 5):

$$\underline{h} = \frac{1}{1 + \underline{e}^{-Z}}$$

where $\underline{Z}$ = constant + $\underline{B}$ (variable 1) + $\underline{B}$ (variable 2) + $\underline{B}$ (variable n; Table 5). The probability that the site is on a wolf hunting route increases if the coefficient in Table 5 is positive and decreases if it is negative. Greater slope, lower levels of hiding cover, lower levels of NDVI, and a lesser distance to the edge of the size class patch increased the probability that a site was along a wolf hunting route. Occurrence within the lowest canopy cover

Table 5. Logistic regression results from wolf travel route vs home range comparison in and near Glacier National Park, Montana, 1994-96.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
Cover Type			0.078	0.106
Open	0.322	0.582		0.580
Ice	1.836	1.384		0.185
Burnt	-1.206	0.665		0.070
Decid.	0.663	0.676		0.324
Larch/Pond. Pine	-0.716	0.651		0.272
Douglas Fir	0.108	0.608		0.859
Lodgepole Pine	-1.097	0.444		0.013
Upland Spruce	0.319	0.415		0.442
Lowland Conifer.	-0.232	0.485		0.632
Hiding Cover	-0.134	0.042	0.001	0.001
NDVI[3]	-0.00006	12.074	0.000	0.000
Position			0.000	0.000
Valley Bottom	0.459	1.516		0.760
Ravine	-1.311	1.925		0.496
SVLS[4]	-1.861	1.482		0.209
SVMS[5]	-1.259	1.512		0.405
Wide Valley Slope	1.689	1.514		0.264
Ridge	0.074	1.615		0.963
Bench	-0.653	1.478		0.811
Creek	-1.751	1.505		0.244
Other	4.312	11.448		0.706
Canopy			0.005	0.007

Table 6. Continued

0-10%	1.076	0.478		0.024
11-30%	-0.713	0.306		0.020
31-50%	0.197	0.324		0.542
51-70%	0.298	0.365		0.443
71-100%	-0.840	0.423		0.047
Scedge[6]	-0.000	0.002	0.004	0.005
Slope	0.111	0.025	0.000	0.207
Constant	3.280	1.559		0.035

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[1] likelihood ratio P value
[2] P value associated with Wald statistic
[3] Normalized difference vegetation index (Nemani et al. 1993)
[4] Side valley lower slope
[5] Side valley middle slope
[7] distance to edge of size class poygon

class increased and occurrence within the second lowest and the highest canopy cover class decreased the probability that the site was along a wolf hunting route. After collapsing position classes to side valley lower slope, wide valley slope, creek bottom, and other, occurrence on a side valley lower slope or in a creek bottom decreased the probability the site was along a wolf route and occurrence on a wide valley slope increased that probability (Table 6). After collapsing cover type classes to lodgepole pine, burnt timber, and other, occurrence within other increased the probability that a site was along a wolf route. The collapsed model's overall prediction success increased from an initial value of 80.0% to a final value of 84.9% (R^{2logit} = 0.679).

Kill Site Versus Hunting

The difference between depth of deer and wolf tracks was significantly greater along wolf hunting routes than at kill sites (med = 6.5 cm vs med = 3.0 cm; n = 26, Wilcoxen Z = -2.386, P = 0.017). Wolf tracks were marginally shallower along hunting routes than at kill sites (med = 4 vs med = 3; n = 29, Wilcoxen Z = -1.722, P = 0.085). There was no difference in snow depth at kill sites and along wolf hunting routes (med = 21.5 cm vs. med = 22 cm; n = 44, Wilcoxen Z = -0.671, P = 0.502), or in deer track depths at kill sites and along wolf hunting routes (med = 11 cm vs.

Table 6. Logistic regression results from wolf travel route versus home range comparison in and near Glacier National Park, Montana, 1994-96.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
Cover Type			0.004	0.004
Other	0.947	0.302		0.002
Burnt	-0.700	0.471		0.137
Lodgepole Pine	-0.247	0.339		0.467
Hiding Cover	-0.138	11.655	0.004	0.000
NDVI[3]	0.00004	11.244	0.001	0.000
Position			0.000	0.272
Other	0.206	0.740		0.000
SVLS[4]	-1.176	13.394		0.000
Wide Valley Slope	2.161	28.418		0.000
Creek	-1.190	0.374		0.002
Canopy			0.001	0.002
0-10%	1.292	0.421		0.002
11-30%	-0.679	0.289		0.019
31-50%	0.128	0.302		0.672
51-70%	0.129	0.330		0.697
71-100%	-0.870	0.378		0.022
SCedge[5]	-0.000	0.000	0.006	0.000
Slope	0.075	0.018	0.000	0.000
Constant	2.230	0.582	0.000	

[1] likelihood ratio P value

[2] P value associated with Wald statistic

[3] normalized difference vegetation index (Nemani et al. 1993)

[4] Side valley lower slope

[5] Distance to edge of size class polygon

med = 11 cm; $\underline{n}$ = 35, Wilcoxen $\underline{Z}$ = -0.411, $\underline{P}$ = 0.681).

Wolves killed deer at sites with more deer (MW $\underline{Z}$ = -9.166, $\underline{P}$ < 0.001) and less elk (MW $\underline{Z}$ = -3.658, $\underline{P}$ = 0.0003) and moose (MW $\underline{Z}$ = -2.913, $\underline{P}$ = 0.0036; Table 4) than was found along travel routes. Hiding cover was greater at kill sites than along hunting routes (MW $\underline{Z}$ = -3.50, $\underline{P}$ = 0.0005). Kill sites had less slope than hunting routes (MW $\underline{Z}$ = -2.51, $\underline{P}$ = 0.012). A greater proportion of kill sites were non-vegetated or were dominated by young trees, while a lower proportion of kill sites were dominated by the pole/sapling size class than were sites along wolf routes (Table 2). More wolf kills were made on ice and in upland spruce cover types than was available along hunting routes (Table 1). Fewer kills were made in burnt timber and in lodgepole pine cover types than was available along hunting routes. More wolf kills were also located in the valley bottom or in ravines (Table 3) than was available along hunting routes. Wolves killed deer at sites with greater NDVI (MW $\underline{Z}$ = -3.92, $\underline{P}$ = 0.0001) and at sites closer to water (MW $\underline{Z}$ = -1.79, $\underline{P}$ = 0.073; Table 4) than was available along hunting routes.

<u>Logistic regression</u>.--

The simplest multivariable model that predicted (χ^2 = 45.17, 5 df, $\underline{P}$ < 0.00001) the probability that a site along a wolf hunting route would be a kill site used hiding cover, distance to water, slope, and position (Table 7). Greater hiding cover, greater distance to water, and less slope

Table 7. Logistic regression results from wolf kill site versus travel route in and near Glacier National Park, Montana, 1994-1996.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
Hiding Cover	0.136	0.034	0.000	0.000
Slope	-0.049	0.018	0.008	0.008
Position			0.017	0.013
Other	-1.127	0.379		0.004
Ravine	1.117	0.666		0.094
Creek	0.010	0.483		0.983
Stream distance	0.002	0.000	0.001	0.000
Constant	-2.811	0.577		0.000

[1] likelihood ratio P value

[2] P value associated with Wald statistic

increased the probability that the site was a kill site. When position categories were collapsed into ravine, creek bottom, and "other," occurrence within a ravine marginally increased the probability that the site was a kill site and "other" decreased that probability. The model overall prediction success increased from an initial value of 87.3% to a final value of 88.4% ($\underline{R}^{2\text{logit}} = 0.154$).

When only data from 1993 were used, the simplest multivariable model that predicted ($\chi^2 = 32.69$, 7 df, $\underline{P} < 0.00001$) where kills would occur along wolf hunting routes used density of elk, hiding cover, and structure (Table 8). A lower density of elk increased the probability that the site was a kill site. The model's overall prediction success increased from an initial value of 80.4% to a final value of 95.7% ($\underline{R}^{2\text{logit}} = 0.719$).

Wolf Kill Site Versus Control Site

There was no difference between kill sites and control sites in snow depth (med = 28 cm vs. med = 29 cm, $\underline{n} = 71$, Wilcoxen $\underline{Z} = -0.674$, $\underline{P} = 0.500$), deer track depth (med = 14.5 cm vs med = 16, $\underline{n} = 50$, Wilcoxen $\underline{Z} = -0.477$, $\underline{P} = 0.633$), wolf track depth (med = 0.5 cm vs. med = 0.5, $\underline{n} = 16$, Wilcoxen $\underline{Z} = -1.54$, $\underline{P} = 0.124$), or in the difference between wolf and deer track depths (med = 0.0 vs. 0.0, $\underline{n} = 16$, Wilcoxen $\underline{Z} = -1.12$, $\underline{P} = 0.26$).

The only differences between kill sites and control

Table 8. Logistic regression results from wolf kill site versus travel route comparison in and near Glacier National Park, Montana, 1993.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
Elk track/km	-2552.7	1276.8	0.000	0.050
Structure			0.001	0.516
Bare	-2.216	205.3		0.991
Herb	-1.934	130.9		0.988
Shrub	-24.189	173.6		0.889
Pole	9.268	178.3		0.957
Young Tree	19.071	178.4		0.915
Hiding Cover			0.012	0.400
0-10%	18.060	205.3		0.930
11-50%	-5.779	102.6		0.955
51-100%	-12.317	102.7		0.905
Constant	-3.489	85.3		0.967

[1] likelihood ratio P value

[2] P value associated with Wald statistic

sites were that kill sites had less slope than control sites (MW $Z = -2.37$, $P = 0.018$; Table 4), and kill sites were marginally farther from deer trails than were control sites ($t = 1.65$, $P = 0.10$).

Logistic regression.--

No independent variables entered the logistic regression comparing wolf kill sites and control sites. When only data from 1993 were utilized, the simplest multi variable model that predicted ($\chi^2 = 42.29$, 12 df, $P < 0.00001$) where kills would occur within a 500 m radius area used structure, hiding cover, canopy, and density of deer (Table 9). A lower density of deer and a greater amount of hiding cover increased the probability that the site was a kill site. Greater levels of structure and canopy increased the probability that the site was a kill site. The model's overall prediction success increased from an initial value of 58.7% to a final value of 82.5% ($R^{2logit} = 0.495$).

Wolf Kills Versus Cougar Kills

There was no difference between wolf kill sites and cougar kill sites in snow depth (med = 32.0 cm vs. med = 23.0 cm, $n = 25$, Wilcoxen $Z = -0.257$, $P = 0.791$), deer track depth (med = 14.0 cm vs med = 15.5, $n = 16$, Wilcoxen $Z = -0.026$, $P = 0.979$), wolf/cougar track depth (med = 4.0 cm vs. med = 5.0, $n = 13$, Wilcoxen $Z = -0.56$, $P = 0.576$), or track depth difference (med = 4.5 vs. 4.5, $n = 12$, Wilcoxen Z

Table 9. Logistic regression results from wolf kill site versus control site comparison in and near Glacier National Park, Montana, 1993.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
Canopy			0.003	0.229
0-10%	-3.041	8.744		0.728
11-30%	8.586	34.725		0.805
31-50%	-3.492	8.716		0.689
51-70%	-1.741	8.714		0.842
71-100%	-0.311	8.727		0.972
Deer track/km	-16.720	10.216	0.065	0.101
Hiding Cover			0.000	0.162
0-10%	-13.631	52.125		0.794
11-50%	5.558	26.063		0.831
51-100%	8.073	26.072		0.757
Structure			0.000	1.000
Bare	25.533	112.69		0.821
Herb	16.489	60.945		0.787
Shrub	-14.167	87.586		0.872
Pole	-4.841	40.946		0.906
Young Tree	-4.728	40.932		0.908
Mature Tree	-18.236	102.93		0.859
Constant	1.448	32.739		0.965

[1] likelihood ratio P value

[2] P value associated with Wald statistic

= -0.71, $\underline{P}$ = 0.48).

Slope was less at wolf kill sites than at cougar kill sites (MW $\underline{Z}$ = -2.36, $\underline{P}$ = 0.018; Table 4). A lesser proportion of wolf kills than cougar kills were in mature trees and a greater proportion were in non-vegetated areas and on ice (Table 2). A higher proportion of wolf kills than cougar kills were made in the lowest canopy cover class and a lower proportion were made in the highest canopy cover class (Table 10) and a lower proportion of wolf kills than cougar kills were made on lower slopes of side valley bottoms (Table 3).

Wolf kills were located farther from the edge of size class polygons (MW $\underline{Z}$ = -2.36, $\underline{P}$ = 0.018) and were marginally farther from trails (MW $\underline{Z}$ = -1.75, $\underline{P}$ = 0.08; Table 4) than cougar kills were.

Density of deer at wolf kill sites in 1993 (med = 25 tracks/km, $\underline{n}$ = 19) was marginally lower than density of deer at cougar kill sites (5 tracks/km, $\underline{n}$ = 56; MW $\underline{Z}$ = -1.62, $\underline{P}$ = 0.10).

Logistic regression.--

The simplest multi variable model that predicted (χ^2 = 8.04, 1 df, $\underline{P}$ < 0.005) the probability that the kill was made by a wolf and not a cougar used distance from water (Table 11). The probability that a deer was killed by a wolf increased the farther the kill was from water. The model overall prediction success increased from an initial

Table 10. Canopy cover (93 method) at wolf kills, cougar kills, control sites, and along systematic routes in and near Glacier National Park, Montana for winter 1993-1996.

% Canopy Cover	Proportion of occurrence at wolf kill	Proportion of occurrence at control	Proportion of occurrence at wolf route	Proportion on systematic
0-10	0.29 (30)[a]	0.28 (22)	0.23 (15)	0.21 (21)
11-30	0.21 (22)	0.20 (16)	0.31 (20)	0.28 (29)
31-50	0.18 (18)[a]	0.19 (15)	0.20 (13)	0.28 (28)
51-75	0.25 (26)	0.27 (21)	0.20 (13)	0.18 (18)
76-100	0.07 (7)	0.06 (5)	0.05 (3)	0.06 (6)

% Canopy Cover	Proportion of occurrence cougar kill[b]	Proportion of occurrence at control site[c]
0-10	0.07 (5)[ad]	0.21 (7)[d]
11-30	0.20 (15)	0.12 (4)
31-50	0.37 (28)[a]	0.39 (13)
51-75	0.24 (18)	0.24 (8)
76-100	0.13 (10)	0.03 (1)

[a] $\underline{P} = 0.003$

[b] Significant difference ($\chi^2 = 19.72$, 4 df, $\underline{P} < 0.0006$) between wolf kill and cougar kill

[c] Significant difference ($\chi^2 = 7.62$, 4 df, $\underline{P} = 0.10$) between cougar kill and control site

[d] ($\underline{P} = 0.01$)

Table 11. Logistic regression results from wolf kill site versus cougar kill site comparison in and near Glacier National Park, Montana, 1994-1996.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
Stream distance	0.002	0.000	0.005	0.009
Constant	-0.591	0.324		0.068

[1] likelihood ratio P value

[2] P value associated with Wald statistic

value of 52.1% to a final value of 68.1% ($\underline{R}^{2logit} = 0.061$).

When only data from 1993 was utilized, the simplest multi variable model that discriminated ($\chi^2 = 8.04$, 2 df, $\underline{P} < 0.018$) wolf kills ($\underline{k}$) from cougar kills used area of size class patch and density of deer tracks (Table 12). Greater area of size class and greater density of deer marginally decreased the probability that the site was a wolf kill. The model's overall prediction success increased from an initial value of 69.8% to a final value of 75.5% ($\underline{R}^{2logit} = 0.125$).

Cougar Kill Sites Versus Cougar Control Sites

There was no difference in snow depths between cougar kill sites and control sites (med = 22.0 vs med = 23.0, $\underline{n} = 34$; Wilcoxen $\underline{Z} = -0.87$, $\underline{P} = 0.38$) or in deer track depths between kill sites and control sites (med = 13.0 vs med = 10.0, $\underline{n} = 21$; $\underline{Z} = -1.17$, $\underline{P} = 0.24$).

Density of deer was lower at cougar kill sites (MW $\underline{Z} = -3.30$, $\underline{P} = 0.001$; Table 4) than at control sites, and the distance to cervid trails was greater at cougar kills than at control sites (MW $\underline{Z} = -1.87$, $\underline{P} = 0.061$; Table 4). Cougar kill sites had a lower proportion of the lowest canopy cover class than control sites (Table 10).

Logistic regression.--

The simplest multi variable model that predicted ($\chi^2 = 8.04$, 1 df, $\underline{P} < 0.005$) the probability that a site within a

Table 12. Logistic regression results from wolf kill site versus cougar kill site in and near Glacier National Park, Montana, 1993.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
Deer track/km	-7.668	4.580	0.093	0.094
Size Class Area	-0.002	0.000	0.008	0.014
Constant	2.117	0.617		0.000

[1] likelihood ratio P value

[2] P value associated with Wald statistic

500 m radius area would be a cougar kill site used density of deer tracks (Table 13). The probability that a cougar would make a kill at a particular site within a 500 m radius area decreased with a higher density of deer. The model overall prediction success increased from an initial value of 69.2% to a final value of 72.3% ($\underline{R}^{2logit} = 0.057$). We did not run a model for 1993 because only 26 cases were available.

DISCUSSION

The primary "habitat" requirement for wolves, an apex predator, is an abundance of prey and security from human-caused mortality (Mech 1995). Because of this, studies of wolves have appropriately focused on predator/prey relationships. Bergerud et al. 1983, Van Ballenberghe 1987, and Dale et al. 1994, however, suggest that at a finer scale of analysis many factors affect the numerical and functional response of wolves to prey . These factors include habitat and spatial variables that affect hunting success of wolves by affecting vulnerability of prey. Habitat and spatial factors certainly affect encounter rates, detection rates, and capture rates of predators (Curio 1976, Taylor 1984). That wolves should select areas for hunting that are profitable in terms of prey is obvious. They should also select areas where they are most likely to be successful at detecting and capturing prey. Some predators may even selectively hunt in areas with lower densities of prey

Table 13. Logistic regression results from cougar kill site versus control site comparison in and near Glacier National Park, Montana, 1994-96.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
Deer track/km	-16.159	7.821	0.031	0.039
Constant	1.262	0.358		0.000

[1] likelihood ratio P value

[2] P value associated with Wald statistic

because those areas offer greater opportunities for success (Messier and Barrette 1985, Murray et al. 1994). Relatively little is known about factors other than prey condition that affect wolf hunting success. Habitat factors affecting hunting success have been more apparent for predators like felids that rely on stealth (Kleiman and Eisenberg 1973, Hornocker 1970, Elliot et al. 1977, Logan and Irwin 1985, Kruuk 1986, Sunquist and Sunquist 1989, Stander and Albon 1993).

Scales of Selection

At the coarsest scale of analysis (landscape or regional), of the variables examined by (Mladenoff et al. 1995), low road density appeared to best explain habitat preference of wolves in the upper midwest. The relationship between habitat preference and prey abundance was not clear. Density of deer was not different between selected and non-selected areas but density of deer was not limiting across the study area, and the highest densities of deer were associated with the highest human impact areas (Mladenoff et al. 1995). Preliminary evidence from Montana does not indicate that wolves prefer areas most remote from human influence, but does, perhaps, indicate selection for areas with relatively high densities of white-tailed deer (K Kunkel pers. obs.).

As a complement to our work, Singleton (1995) analyzed the home range selection by wolves within the North Fork (NF) basin. He found that wolves in the NF selected the main valley bottom and lower slopes in side valleys. This corresponded with cervid wintering areas. For their home ranges, wolves in the NF selected flat areas and slight slopes, areas greater than 0.5 km from water, and lower road densities. No clear selection for a particular cover type was detected.

At the next finer scale of analysis (travel route within wolf territory), Singleton (1995) found that wolves selected main valley bottoms and lower slopes in the main valley. Wolf use increased as slope, distance from water, and distance to roads decreased. The deciduous cover type, non-forest type, and burn type increased the probability that a point was along a travel route and the coniferous and lodgepole pine forest classes decreased that probability. Southwestern aspects increased the probability that a point was along a wolf travel route.

Our analysis used stricter criteria than Singleton (1995) for availability of spatial and habitat features within wolf home ranges, and our data were collected at the site. We sampled those areas that were likely to be used by wolves for travel (roads, trails, and waterways within the home range; see above). We selected these areas because much of the area defined by the minimum convex polygon method for determining home range (used by Singleton) was not used by wolves (Appendix B in Singleton 1995). Results from our study were generally similar to those of Singleton (1995) except our finding that wolves traveled more in areas with greater slope than was available. This probably results from the difference in scale; more areas with steeper slopes were available within the home range than were available in the areas we sampled. The travel selection patterns of wolves outlined above from this study and from Singleton (1995) are probably best explained by wolf selection for routes that are easiest to travel and routes that are in cervid concentration areas. Topographic class selection is likely related to prey availability, as is selection for sites with greater slope because deer also select these areas due to reduced snow depths (Pauley et al. 1993, K. Kunkel, unpubl. data). Selection for lowland spruce probably corresponds to selection by deer for this cover type (Jenkins and Wright 1988). Ease of travel, however, could also explain these preferences. Selection for the burnt timber cover type is probably related to ease of travel. Selection for areas closer to edges of size class patches likely corresponds to deer selection for these areas (Keay and Peek 1980, Krahmer 1989) and/or ease of travel by wolves (Bergerud 1981).

We were able to compare several variables Singleton (1995) could not. We found that wolves selected areas for travel with greater densities of deer and lower densities of elk. The most abundant prey in the NF is white-tailed deer (chapter 1) and wolves concentrated their hunting in white-tailed deer winter ranges where elk were less abundant (Bureau 1992, chapter 4). Wolves selected elk over deer as a prey species in our study area (chapter 4) but probably selected to hunt in deer winter ranges because these were more predictable than elk wintering areas (Bureau 1992, chapter 4).

Wolves selected areas with lower snow depths for travel, probably for the greater ease of travel that they provide or because prey also selected areas of reduced snow depth. Spatial variation in snow depths apparently did not affect vulnerability of deer to wolf predation, as indicated by the absence of any difference in snow depth between kill sites and travel routes and kill site and control sites. That snow depth affects prey vulnerability on a temporal scale (i.e. among winters and over the course of a winter) is well established (Mech and Frenzel 1971, Mech and Karns 1977, Peterson 1977, Nelson and Mech 1986, Fuller 1991). Wolf travel routes, kill sites, and control sites all occurred primarily within deer winter ranges and along the deer trails therein. As a result, the role of snow in affecting deer vulnerability is very limited, at least within the range of snow depths occurring during our study. We are not aware of any published study, prior to ours, that has demonstrated the assumed effect of snow hinderance on deer escape. No published study has compared snow depth at kill sites to depth at random nearby sites. Nor has any study shown higher hunting success rates of wolves or higher mortality rates of deer prior to late winter (when deer are in poorer physical condition) in winters of greater snow depths. Deer rely on packed trails within winter ranges to escape wolves (Nelson and Mech 1993, Messier and Barrette 1985). Depth of deer tracks along these trails vary little (K. Kunkel pers. obs.). Huggard (1993a) reported that wolf chases of elk were short regardless of snow depth and postulated that deeper snow acted primarily to increase encounter rates with elk rather than to increase wolf hunting success. Snow depth did not significantly affect kill rates of wolves on caribou in Gates of the Arctic National Park (Dale et al. 1995). Based on results from our studies and those of previous research, we suggest that the primary effect of snow on deer vulnerability is the reduction in food availability and the resulting poorer condition of deer, which reduces their physical ability to escape predation. This is not to say that deep snow or the right crusting conditions don't reduce the ability of deer to escape wolves, but that the behavioral adaption of deer to "yard" during winter greatly reduces the opportunity for this to occur. Yarding behavior may result in decreased vulnerability of deer relative to elk and even moose in early winter especially in deep snow winters (Telfer and

Kelsall 1984). The latter 2 species may be hindered by deep snow during escape from wolves. This may have important implications for selection of prey by wolves in multi-prey systems where deer are present. We think, however, that the effects of snow on deer physical condition may be an overriding factor (chapter 2).

Wolves also selected areas with lower levels of hiding cover for travel. A closer look at selection of hiding cover class revealed that wolves were selecting for travel in the lowest hiding cover class (most open) and against travel in the highest cover class (most closed). As with snow depth, wolves may be selecting for easy areas to travel in (more open), and for areas with the greatest visibility for detecting prey. The benefit of these 2 factors apparently outweighs the value of the greater vulnerability of deer to wolves in areas of high hiding cover (see below). Wolves probably spend a greater proportion of time searching for prey rather than actually approaching prey (Mech 1966). Deer probably use habitat with lower hiding cover disproportionately because they are safer from wolves and cougars there; thus wolves are forced to search these areas. As a result, wolves must work harder in these areas to find stalking cover to approach deer within distances they can successfully pursue them.

Wolves were more successful killing deer in denser hiding cover. A primary antipredator strategy of white-tailed deer is to detect predators and keep their approach distance maximized so that they can quickly outdistance the pursuing predator (Mech 1966, Mech 1970, Mech 1984, Lingle 1992). Differences in alert behavior indicate that deer in dense vegetation are more wary than deer in open areas (LaGory 1987). Experiments in our study area showed that deer spent greater amounts of time and expended greater effort feeding in areas with less hiding cover (lower "giving-up-density"; sensu Kotler et al. 1994, chapter 5). The lower "giving-up-density" in areas of lower hiding cover indicate deer are less wary there and thus may be safer in these habitats (Kotler et al. 1994). Deer can often detect wolves before wolves detect them (Mech 1966). Greater than 90% of the observations of wolves hunting deer and moose in Minnesota resulted in escape by the prey (Nelson and Mech 1993). Hornocker (1970), Seidensticker (1973), and Logan and Irwin (1985) have hypothesized that cougars achieve greater hunting success in areas with habitat features that provide concealment although we are aware of no published studies prior to ours verifying this (see below). In comparison, canids may achieve greater hunting success in areas generally lacking vegetative cover (Wells and Bekoff 1982). In Yukon Territory, however, coyotes selected denser habitats than lynx (Murray et al. 1994). Coyotes were more successful hunting hares in dense habitats than more open habitats, probably because these habitats allowed coyotes to approach hares to within killing distance (Murray et al. 1995). This strategy may have been selected because the sustained speed of coyotes did not permit successful capture (Curio 1976). The same may be true for wolves chasing deer in deer yards (Nelson and Mech 1993). The availability of escape trails and the confusion provided by other deer likely produce escape advantages for deer (Sweeney et al. 1971, Geist 1981, Nelson and Mech 1981). For hunting dogs (Lycaon pictus), the group size of gazelles (Gazelli thomsoni), height of surrounding vegetation, and group size of hunting dogs had little effect on hunting success (Fanshawe and Fitzgibbon 1993). Even so, reduced flight distance of male gazelles probably was the most important factor accounting for the higher rates of hunting success on this group (Fanshawe and Fitzgibbon 1993). Wolves certainly are capable of killing prey in areas without stalking cover, but we believe that when they hunt white-tailed deer concentrated in yards, they are much more successful when they can closely approach their quarry without detection.

Within winter yards, deer exhibit 2 levels of antipredator responses which correspond first to avoiding encounters and detection and second to avoiding pursuit and subduction. In the absence of wolves, deer use more open habitats that provide foraging and probably reduced exposure to cougars (chapter 5). When wolves move into a yard to hunt, deer spaced away from high wolf use areas and concurrently moved into denser cover to avoid encounters and detection by wolves (chapter 5). At the next level, they avoid pursuit and subduction by using sites where stalking cover is lowest.

Wolves killed more deer in areas of higher deer density than was available along their travel routes. This may simply indicate that in all areas wolves frequent, they are more likely to be successful where encounter rates are greater. Most kills we located were in deer yards (chapter 4). When compared to control sites, density of deer tracks was lower (but not significantly) at kill sites in 1994-1996, but in 1993 density was significantly lower at kill sites. This may indicate that wolves are more successful killing in portions of yards with lower deer density. Snow depths were greater in 1993 (see below) and deer may have been more susceptible in lower density areas where there were fewer trails for escape. Deer appeared to be more vulnerable to predators on the edges of deer yards or in lower deer density areas in northwestern Minnesota (Fritts and Mech 1981) although the boundaries of the yards and distribution of deer within them were not well defined. Kolenosky (1972) reported that a greater proportion of kills were made along edges of yards, although the methodology used to determine deer concentration was not provided nor were data on number of kills among areas of differing densities. Unlike our study, neither of those studies directly assessed density of deer at kill sites. Messier and Barrette (1985) provided convincing evidence that deer were more vulnerable to coyotes in areas of lower deer density. Coyotes, however, depend on the opportunity to "quarry deer in deep snow where the animal is harassed until exhausted" (Messier and Barrette 1985, p. 787). Wolves typically do not require such conditions to kill deer.

Substantial evidence exists for the antipredator benefits accrued by deer concentrating in winter yards (Geist 1981, Nelson and Mech 1981, Mech 1984, Messier and Barrette 1985, Nelson and Mech 1993). The primary means by which those benefits are accrued are unknown, but may include ease of escape along runways, increased predator detection, greater predator confusion during pursuit, sharing of predation risk (lower predator:prey ratios), and familiarity of escape terrain. An additional benefit that has not been discussed is the increased transfer of information among deer and their resulting behavioral response (increased alertness and shift in use of habitat). Such behavior reduces vulnerability of all deer in the yard and may force the predator to hunt elsewhere (resource depression; Charnov et al. 1976, chapter 5). All of these factors probably play some role. Their respective importance may also vary by particular habitat and physiographic factors of specific yards and among winters of varying severity. Fuller (1991) found only half as many kills in or on edges of concentration areas during mild versus severe winters. Messier and Barrette (1985) believed that density of runways was the most influential element for deer/coyote systems. Based on the relatively high survival of dispersing deer, Nelson and Mech (1991) believed that site familiarity may have relatively little effect on deer survival. Sites where deer were killed by wolves in our study were marginally farther from a deer trail than control sites, pointing to the importance of the trail system for escape.

In addition to comparison with random points within the home range, Singleton (1995) also compared habitat variables collected at points along travel routes to "control" points located 250 m perpendicular from the travel route. This scale of analysis may be an indication of selection by wolves for areas that improve hunting success. Wolves selected flatter areas for travel than were available at control sites. We found that deer were more likely to be killed by wolves on flatter terrain. There may be several reasons for this. Slopes may allow deer to better detect and avoid wolves. Bibikov (1982) reported that when prey were above wolves on a slope, wolves did not attack and if red deer (Cervus elaphus) ran uphill, wolves didn't pursue. Similar behavior has been described by Murie (1944) in wolves hunting bighorn sheep (Ovis canadensis) and caribou (Rangifer tarandus). Prey running downhill may be more likely to become injured (Bibikov 1982) and then killed by wolves at the bottom of the slope. One antipredator strategy of mule deer (Odocoileus hemionus) is to run or bound up steep slopes away from predators (Geist 1981). Geist (1981) postulated that because vertical locomotion is 12 times more costly than horizontal locomotion, mule deer run uphill to impose an unacceptably heavy energetic cost on pursuing predators. When measuring flight responses of white-tailed deer to humans, we often observed them running uphill (K. Kunkel, unpubl. data) although Geist (1981) believed that white-tailed deer more typically ran downhill in response to predators. Bibikov (1982) believed that wolves may appraise condition of prey by whether they run up or downhill, the latter indicating poorer condition. When running downhill, more deer may be killed when they reach the bottom of the slope if it ends in a ravine or on ice (Formozov 1946 [cited in Bibikov 1982], Sludskii 1962 [cited in Bibikov 1982], Pimlott et al. 1969, Kudaktin 1978 [cited in Bibikov 1982], Bibikov 1982, Mech 1984). More deer in our study were killed in ravines than at other topographic classes and more were killed closer to water.

We found more deer killed on ice than in other cover types. Wolves have greater mobility on ice than do deer (Mech and Frenzel 1971) and deer are therefore probably easier to kill there.

Cougar vs wolf

Prey living in multi-predator environments are faced with additional hazards and greater challenges and conflicts in avoiding predators than their counterparts facing only one predator. This is particularly true for deer facing their 2 most dangerous predators in North America, wolves and cougars. Even though most prey live with multiple predators, little research has examined behavioral responses of prey to this and none has examined this for cervids in North America (for review see Lima 1992).

Cougars are generally more habitat-specific than wolves, probably because they require some degree of topography or vegetation to successfully stalk or ambush prey (Hornocker 1970, Seidensticker 1973, Logan and Irwin 1985), although no published research prior to our study has examined this requirement directly or quantitatively. Cougars killed more deer than wolves in areas with greater canopy and more mature trees and they killed fewer deer than wolves in non-vegetated areas. Cougars killed more deer on steeper slopes and closer to water than did wolves. The latter may indicate the importance of cover in riparian areas, or broken topography (Logan and Irwin 1985). Cougars also killed more deer in size class patches greater in area than wolves did. This may indicate the affinity of cougars for large continuous blocks of cover and the preference of wolves for edges or more heterogenous habitat.

Cougars killed deer marginally closer to trails than wolves did, possibly indicating the value of ambush sites along trails. Trails are probably predictably traveled by deer. Cougars also killed deer in areas of greater deer density than did wolves. The benefits of yarding by deer may not be as profound in the face of cougar predation as they are for wolf predation, although density of deer was lower at cougar kill sites than at control sites and the distance to a deer trail was greater at kill sites. Cougars were more successful in areas of greater deer density than were wolves, but deer were less vulnerable to both predators in the highest deer density areas. Detection of predators is key to avoidance of both wolf and cougar predation. Reduced stalking cover and presence of conspecifics are primary factors increasing the odds of detection. It seems likely that vigilance behavior adaptive for detection of wolves would also apply to cougars, but this remains to be tested (sensu Lima 1992). However, it is possible that because predators may form search images for prey, the opposite may also be true.

Antipredatory behavior that reduces mortality from one predator may not reduce it for another and may even increase it (predator facilitation; Charnov et al. 1976, Kotler et al. 1992, Korpimaki et al. 1996, chapter 5). Deer may use very open habitats to avoid cougars but they are restricted from doing this to a large degree by snow depths, and they are also vulnerable to wolves in these areas. Deer may use large contiguous blocks of mature conifers to avoid efficient searching by wolves but they are vulnerable to cougars in this type of habitat. Deer may use steeper slopes to avoid wolves but they become more susceptible to cougars there. The behavioral response of deer should be tilted toward the strategy that reduces exposure to the most dangerous predator, but in our study area, wolf-caused and cougar-caused mortality rates on deer were nearly equal (chapter 2). More work is needed on predator-specific responses of deer to fine-tune potential management strategies.

Effects of Winter Severity

Severity of winter apparently had very important effects on factors affecting vulnerability of deer. The winter of 1993 was more severe (105 days > 30 cm snow) than the winter of 1994 (70 days) or the winter of 1995 (74 days). Based on telemetry locations, deer were more concentrated in yards (winter ranges) and used areas with lower snow depths relative to other areas (K. Kunkel unpubl. data) during the more severe winter. Distribution of wolf locations reflected this (chapter 4). Deer density at sites with > 50% canopy cover was greater in 1993 (med = 24.0 tracks/km, SD = 54.5, $\underline{n}$ = 60) than in 1994 (med = 8.2 tracks/km, SD = 58.6, $\underline{n}$ = 42; MW $\underline{Z}$ = -2.68, $\underline{P}$ = 0.007) while deer density at sites with < 50% canopy cover was marginally less in 1993 (med = 4.2 tracks/km, SD = 62.6, n = 97) than 1994 (6.9 tracks/km, SD = 78.3, n = 112; MW Z = -1.65, P = 0.09). Deer density at sites with > 50% canopy cover in 1993 was also greater than 1995 (med = 2.4, SD = 43.8, n = 21; MW Z = -2.71, P = 0.007) while there was no difference between deer density at sites with < 50% canopy between 1993 and 1995 (med = 4.5, SD = 30.1, n = 76; MW Z = -0.41, P = 0.68). Deer density at sites with > 50% canopy cover did not differ between 1994 and 1995 (MW Z = -1.20, P = 0.228) but was lower in 1995 than 1994 at sites with < 50% canopy cover (MW Z = -1.91, P = 0.056). These findings were similar to those reported by others; deer use conifer cover less and were more dispersed in milder winters and were also more difficult for wolves to capture (Rongstad and Tester 1969, Jackson and Sarbello 1980, Fuller 1991). Consequently, wolves may change habitat use patterns during milder winters and may spend more time in deciduous cover where snow may be deeper (Fuller 1991). We conclude that during more severe winters the antipredator benefits of yarding are increased.

Logistic Models

The improvement in correct classification of sites and the $R^{2\text{logit}}$ values in the logistic models we developed were significant but generally low. Most of this probably results from model misspecification (e.g. possibly not including prey condition parameters in the model). We believe these models and the results of our univariate tests are theoretically important, but the application value remains to be tested. We advocate applying the recommended prescriptions (see below) as experiments conducted as integral parts of management programs (MacNab 1983, Walters and Holling 1990, Clark and Nudds 1991) that include measuring wolf and cougar predation rates and/or deer survival rates.

CONCLUSIONS

The element of surprise appears to be a very important factor affecting success of both wolves and cougars in our study. The value of this parameter has generally been assumed for cougars due to their hunting technique. Prior to our work, only anecdotal evidence existed for the value of surprise to wolves. Prey condition was assumed to be the primary factor affecting success. The relative value of predator detection and prey quality could not be evaluated in our study, but Kenward (1978) showed that surprise interacted with prey condition to determine attack success (of goshawks [Accipiter gentilis] on pigeons [Columba palumbas]), each being the dominant factor at times.

We found that habitat and landscape features affected wolf hunting success and therefore probably affected the functional response of wolves. Whether these features can be manipulated to affect the kill rate of wolves remains to be tested. Such manipulations may simply result in greater hunting efforts by wolves (longer and more careful searches; McCullough 1979, Wood and Hand 1985) to maintain the same kill rate, or they may result in changes in prey selection patterns (i.e. killing of poorer condition prey; Potvin et al. 1988).

Very little is known about how habitat and landscape features in the Rocky Mountains (or anywhere) affect security of cervids from predators. "There are many interrelationships between the habitat type normally occupied by a species and .. [its] antipredator behavior... The choice of habitat is perhaps one of the most basic behaviorally mediated processes in an animal's life, yet we know virtually nothing about the mechanisms involved (Leuthold 1977; cited in Prins and Iason 1989). Few decisions an animal makes are as critical as predator avoidance. As a result, Lima and Dill (1990) believed that almost all behavior and habitat use should be viewed as avoidance of predation. Alternately, Prins and Iason (1989) believed that buffalo (_Syncerus c. caffer_) largely ignored lion (_Panther leo_) and selected habitats without taking risk into account. We examine this for deer in more detail elsewhere (chapter 5). Most studies of habitat preference tell us nothing about whether the habitats are critical for survival (White and Garrott 1990). We believe our study is a first step in this direction. We have provided evidence indicating habitats that have lower probabilities of predator-caused mortality for deer. Failure to avoid predation has an immediate and critical implication: death. The next step will be to manipulate habitats in the directions indicated below and monitor resulting survival rates of cervids or kill rates of predators, and preferably both.

Mitigation of the rate of capture appears to be more important than mitigating encounter and detection rates for white-tailed deer attempting to avoid predation by wolves and cougars during winter. White-tailed deer concentrate in yards where wolves and cougars concentrate their hunting efforts. While deer rely on avoiding encounters and detection by predators, they also rely on being able to readily detect predators and flee before predators can get within successful attack range. Deer in larger groups are more likely to detect the presence of a predator (LaGory 1987, Caro et al. 1995) and larger groups of fleeing animals probably confuse wolves and decrease the likelihood of successful capture (Sweeney et al. 1971, Caro and Fitzgibbon 1992).

MANAGEMENT IMPLICATIONS

We offer several management strategies that might be employed to reduce hunting success of wolves and cougars on white-tailed deer when this is deemed necessary. Similar to Messier and Barrette (1985), we advocate the promotion of large deer yards with high deer density. Few large yards are probably better than several small in the system we studied. Smuts (1978) advocated a similar approach for mobile aggregations of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) in Africa. Additional research is needed to determine how this might be accomplished, given the traditional movement patterns of deer (Nelson and Mech 1981). Predator detection and escape are maximized under this strategy as is resource depression for predators (Huggard 1993*b*, chapter 5). However, predator facilitation may be also be enhanced because under such a strategy wolves are present in the yard for a greater proportion of time (only yard available to hunt). Additionally, the increased presence of hunting wolves may reduce foraging by deer due to their increased levels of wariness. Enhancement of food production in these yards will improve success of the strategy. Foods should be high in nutrition but should not provide large increases in hiding (stalking) cover. Deciduous browse (e.g. *Amelenchier alnifolia*, *Cornus stolinifera*, and *Populus triocarpa*), low evergreen shrubs (*Berberis repens*, *Juniperus* spp.) or lichens (*Bryoria spp.*) would probably be best (Singer 1979, Jenkins and Wright 1987).

Control of fire in the Rocky Mountains has resulted in forest in-growth which has resulted in an increase in stalking cover for predators. This has potentially altered the predator-prey "balance" in certain situations in favor of wolves and cougars. Similar human-caused shifts in balance (disequilibriums) have been hypothesized for declines in waterfowl production (Clark and Nudds 1991), bighorn sheep (Ovis canadensis; Berger and Wehausen 1991), and moose (Bergerud 1981) among others. Prior to the arrival of Euroamericans, lightning-caused and Indian-caused fires produced more open habitats in many portions of the Rockies (Barrett and Arno 1982). In fact, one of the reasons hypothesized for use of fire by Indians was to reduce camouflage for enemies. Smuts (1978) believed that an increase in cover in Kruger Park, South Africa facilitated predation by lions. Prescribed burns in deer winter yards can reduce stalking cover and improve browse production. Fires must be managed to reduce undergrowth and small trees but to maintain snow mitigation structure provided by large trees. Interspersion of more dense pockets of hiding cover should probably be maintained for escape (during pursuit) cover. More research is needed to determine the amount of this type of cover necessary.

Areas surrounding yards should be managed to reduce ease of wolf travel. Contiguous blocks of dense timber with few trails and roads could aid in this. These recommendations are consistent with those of Bergerud (1981) and McNay and Voller (1995).

Peek et al. (1982) lamented the lack of knowledge about the role of security cover in maintaining deer populations. Despite this, management recommendations for white-tailed deer winter range in the Rocky Mountains have largely failed to include the role of predators in habitat selection by deer (Keay and Peek 1980, Jenkins and Wright 1988, Pauley et al. 1993, others, but see McNay and Voller 1995 for black-tailed deer [Odocoileus hemionus]) and thereby have failed to fully answer why deer select habitats they do. This has probably resulted in misspecification of prediction models. In addition to snow mitigation, selection of old growth habitats and their associated understory structure by deer may largely result from optimization of predator detection. Excluding analysis of the role of predators in prey habitat selection and in resulting management recommendations may create especially difficult management scenarios (i.e. prolonged depressed densities of prey) as wolves continue to recolonize the Rockies (Boertje et al. 1996).

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CHAPTER 4: PREY ENCOUNTER, CHOICE, AND RATE OF KILL BY WOLVES IN NORTHWESTERN MONTANA

Abstract: We examined prey species preference, rates of kill, and home range spatial use of recolonizing wolves (*Canis lupus*) in a multi-prey system in northwestern Montana. Wolves selected to hunt in white-tailed deer (*Odocoileus virginianus*) winter ranges/yards and within these areas they selected to kill elk (*Cervus elaphus*) and moose (*Alces alces*) over deer. Snow depth was positively correlated with and best explained the variation in proportion of deer selected by wolves annually. Outside of severe winters, deer, elk, and moose appeared to be similarly vulnerable to wolf predation. Annual kill rate per wolf has increased since wolf recolonization began. Snow depth and wolf density were positively correlated with and best explained the annual variation in the total kill rate of wolves. The proportion of deer selected by wolves was positively correlated with kill rate per wolf. Use of space by wolves reflected their efficient responses to local changes in prey abundance. As wolves continue to recolonize, predator/prey managers may have to modify local prey population objectives. Managers should intensively monitor wolf and prey populations where wolf recolonization is occurring so that timely management responses can be made when necessary.

INTRODUCTION

The wolf population that recolonized northwestern Montana via dispersal has increased approximately 20%/year since the first record of wolf reproduction in 1986 (Ream et al. 1989, Pletscher et al. 1997). As a result, the recovery goal of 10 breeding pairs of wolves for northwestern Montana will soon be reached. Sixty wolves were reintroduced into Yellowstone National Park and central Idaho in 1995-96 and recovery goals may be reached by 2000 in these areas (E.E. Bangs, U.S. Fish and Wildl. Serv., pers. commun.). The continued expansion of wolves in the Rocky Mountains will increase competition among predators, including humans, for available prey (chapter 1). Management of prey and predators will become more complex and controversial. Managers will require more detailed information on factors affecting selection of prey and rate of kill by wolves in the complex predator and prey systems existing in the Rocky Mountains to meet predator and prey population objectives.

Rates of predation by wolves are an important component for modelling predator-prey dynamics and predicting impacts of predation, however they are extremely expensive and difficult to obtain, particularly predation rates on deer (Odocoileus spp.) because of the speed at which they are consumed by wolves (Fuller 1989). Determination of the factors affecting rates of predation could produce a more efficient way of predicting impacts on prey and indicate opportunities for potentially altering predation rates.

The killing rate of wolves varies greatly (Peterson and Page 1987) and is a product of 3 factors: 1) the rate of encounter with prey, 2) the rate of detection of prey, and 3) the rate of capture of prey (Taylor 1984). These factors are affected by components of the landscape and behavior of the prey that place ecological constraints on selection of prey and rate of kill (for review see Skogland 1991). Encounter rate is affected by search pattern of wolves (i.e. wolves concentrating hunts in particular patches); prey density, dispersion, diversity, and social organization; and habitat and physiographic features that may constrain wolf travel (Huggard 1993a, Weaver 1994, chapter 3). Detection rate is affected by activity and habitat use of prey and potentially formation of a search image (Curio 1976). Capture rate is affected by structural features of the habitat (refuges), snow characteristics, escape terrain, interference from other predators, quality of prey, and escape behavior (Skogland 1991, chapter 3). Selection of prey is further affected by profitability, or the ratio of net energy gain to handling time (e/h; Stephens and Krebs 1986; Huggard 1993a). Examination of these components may allow wildlife managers to better predict dynamics between predator and prey and manage these systems more effectively. This information is crucial for the Rocky Mountain systems that are beginning to change dramatically as a result of wolf recovery.

Numerous studies have examined diets of wolves (for review in multi-prey environments see Weaver 1994), fewer have examined selection of food by comparing proportions of species killed to proportions of species available, and very few have determined factors affecting prey selection (Huggard 1993a, Weaver 1994, Mech et al. 1995). Very little is known about why wolves select the prey they do. It is the why questions that are necessary to advance our understanding of mechanisms affecting wolf foraging. Determining why will allow us to make widely applicable predictions regarding the effects of wolves on prey (Gavin 1991, Sinclair 1991).

We studied population parameters, diet, predation rates, and movement patterns of wolves in the North Fork of the Flathead Valley in Montana from 1983 through 1996. A more intensive examination of predator-prey relationships between wolves, white-tailed deer (deer), elk, and moose was conducted from 1990 through 1996 (Bureau 1992, Rachael 1992, Langley 1993, chapter 1, 2, 3, and 5). Our objectives here were to determine factors affecting prey selection and the rate of kill by wolves.

METHODS

We captured, sedated, and radio-tagged wolves following techniques described by Mech (1974) and Ream et al. (1991). Wolves were located from the ground or the air > 4 times/week during winter (Nov-Apr) to locate their travel routes and estimate wolf numbers in each pack. We followed the travel routes on skis, snowshoes, or foot 1-2 days after wolves had moved out of the area. We followed wolf tracks continuously for as long as snow conditions and logistical constraints would allow. Each continuous tracking episode was called a wolf tracking bout. Each tracking bout was traced onto 1:24,000 USGS or 1:50,000 Canadian Dept. of Energy and Mines topographic maps. Compasses, map features, and pacing of distances were used to plot routes on maps. Starting in 1994, global positioning units were sometimes used to reduce mapping error (Singleton 1995). Wolf track bouts were digitized using the geographic information system software PAMAP.

Prey Selection

We skied 2 100 m transects in opposite directions perpendicular to the wolf travel route at 1 km intervals along these routes to estimate relative proportions of prey encountered by wolves. At these intervals, travel pattern of wolves was recorded as either concentrated (wolves traveling single file) or dispersed. The distance to the first deer, elk, and moose track on each transect was recorded; if no track was encountered the distance recorded was 100 m. The number of deer, elk, and moose tracks located on both transects (0, 1, or 2; only the first track on each transect was recorded) was divided by the distance to that track (e.g. 1/190 if one deer track was found at 90 m in one direction and no tracks were found in the opposite direction) to obtain the number of deer, elk, and moose tracks/m. This value was divided by the number of days since the most recent snowfall of > 5 cm to adjust for snowfall effects. We set seven as the maximum number of days since snowfall because after this track deposition had plateaued and tracks started to deteriorate. To estimate prey available throughout wolf territories, we followed the same procedure along systematic transects that followed hiking trails and roads throughout the Camas packs' territories (Fig. 1 and 2, chpt. 1). Manly's (1974) index of selectivity (chapter 1) was used to determine if wolves were selecting for species of prey to encounter along their travel routes.

Diets of wolves were determined by examining kills made by wolves located along wolf tracking bouts following the criteria of chapter 1. Cougar kills were located incidentally while following wolf tracks and by snow-tracking cougars (chapter 1). To determine if wolves were killing individuals of a particular prey species disproportionately to the prey's availability, we calculated Manly's (1974) index of selectivity for each cervid prey species, separately for Montana and Canadian packs. Mule deer (Odocoileus hemionus) were excluded due to small sample size. Packs were analyzed separately because prey available to Montana packs (North and South Camas packs) was predominately white-tailed deer while very few white-tailed deer were available to the Canadian pack (Spruce pack). Availability was determined for both wolf travel routes and for systematic routes based on track transects along each.

Relative Vulnerability of Prey Species

Femur marrow, when present, was collected from each carcass; estimation of fat content followed Neiland (1970) and chapter 1. Diastema and hind foot length were also measured on each carcass when possible.

To compare age classes of deer, elk, and moose killed by wolves and cougars, we classed age as fawn/calf, prime (deer: 1 - 9 yrs, elk: 1 - 11 yrs, moose: 1 - 14 yrs) and old (deer: > 9 yrs, elk: > 11 yrs, and moose > 14 yrs (chapter 2).

We operated the North Fork hunter big game check station each year to estimate hunter success (hunter-days per deer or elk killed). Hunter success is highly correlated with deer and elk population trends (Freddy 1982, Roseberry and Woolf 1991, chapter 2). We also measured the diastema length of yearling male deer coming through the station to estimate trends in condition of deer (Reimers 1972, Frisina and Douglass 1989).

Kill Rate

The annual kill rate of wolves (kill per unit effort) was estimated by dividing the number of wolf kills by the total length of tracking bouts. Some kills were located from the air while locating radiocollared wolves or were located incidentally while conducting other fieldwork. Wolf tracks were then followed away from these kills. The potential bias of including these kills was minimal because the proportion of kills located this way remained similar from year to year. All classes of kills (certain, probable, possible; chapter 1) were used for determining kill rates. The proportion of these classes remained relatively constant among years.

Wolf Space Use

We used multiresponse permutation procedures (MRPP), a nonparametric statistical test (Mielke et al. 1976, chapter 1), to compare distributions of radio locations of wolves and wolf kill sites between years and related this to changes in prey distribution. The *P* values (calculated using program BLOSSOM [Slauson et al. 1994]) indicate the probability that the distribution of these sites/locations was the same.

Based on aerial radio locations of wolves, yearly home range size of each wolf pack was estimated by the 75% contour of the adaptive kernal method (Worton 1989) using

CALHOME (Kie et al. 1996). This method was also used to estimate the size of the yearly kill dispersion area for each pack by using locations of kill sites.

Statistical Analysis

To examine factors affecting prey selection, analysis of covariance was used to compare mean femur marrow fat values among species of prey (adults only) killed by wolves and cougars (*Puma concolor*) using month of death as the covariate. Prey selection patterns of cougars were similar to those of wolves (chapter 1) and so cougar kills were included in this analysis to increase the sample size of kills. Sex, age, and month of death of kills were cross-tabulated by species of prey. We used Pearson Chi-square analysis to test the null hypotheses of independence among categories. When > than 20% of cells had expected values < 5, we combined adjacent categories. Adjusted standardized residuals ([observed - expected/expected$^{0.5}$]/standard error) were used to identify significant cells (Habermann 1973).

Stepwise multiple linear regression was used to compute partial correlation coefficients and *t* statistics to examine independent variables correlated with proportion of deer selected by wolves. Independent variables examined were annual mean femur marrow fat value (from all adult cervids killed by predators), hunter-days/deer killed, hunter-days/elk killed, days/winter with > 30 cm snow (Fuller 1991, Pauley et al. 1993), maximum number of wolves counted in spring (excluding newborn pups), annual mean diastema lengths of yearling male white-tailed deer killed by hunters, and year. The Kruskall-Wallis test was used to compare density of deer and elk tracks (tracks/m) encountered along wolf routes among years.

Stepwise multiple linear regression was also used to compute partial correlation coefficients and t statistics to examine independent variables correlated with total wolf kill rate, kill rate/wolf, total deer kill rate/wolf, and total elk kill rate/wolf. Independent variables examined were the same as those used in the previous regression except for the deletion of annual mean femur marrow fat and year and the addition of proportion of deer selected by wolves. Number of wolves was not included as an independent variable in the kill per wolf analyses. Variables entered the regression model at the 0.05 level and were removed at the 0.10 level.

To determine effects of prey density on shifts in home range use by wolves, we used Mann-Whitney tests to compare median deer pellet groups/plot between yards and between years. In chapter 2 I detail the methods used to estimate trends in deer pellet groups.

RESULTS

We followed 51 radio-tagged wolves in 1-4 packs from August 1984 through May 1995. Pack sizes in May ranged from

2 to 12 wolves. We followed wolves on 284 tracking bouts from 1987 through 1995 for 2,641 km (Table 1). Mean length of bouts ranged from 2.8 km in 1995 to 26.5 km in 1987.

Prey Selection

When compared to availability along systematic route (availability territory-wide), relative densities of prey along wolf travel routes indicated that North and South Camas wolf packs selected for encounters with deer (Manly index = 0.40 ± 0.04) over elk (0.19 ± 0.09; Table 2). Wolves did not select for or against encounters with moose (0.32 ± 1.14; Table 2). The sample size of systematic track transects in the Spruce Pack territory was too small to compare with their hunting routes.

Along their hunting routes, Camas wolves selected to kill elk (0.51 ± 0.04; Table 2) and moose (0.51 ± 0.12) over deer (0.31 ± 0.01). Spruce wolves selected to kill elk (0.37 ± 0.08; Table 2) and killed moose at levels similar to expected based on their availability along hunting routes (0.33 ± 0.05). Spruce wolves did not select for or against killing deer (0.20 ± 0.31).

When compared to availability along systematic routes (availability territory-wide), Camas wolves selected to kill deer (0.37 ± 0.01; Table 2) over elk (0.29 ± 0.02) while moose were killed at levels similar to expected (0.34 ± 0.19).

Table 1. Trend in total wolf kill rate (km traveled/kill), prey density, snow depth (number of days with > 30 cm of snow on the ground), prey selection, and wolf numbers from 1986-1996 in and near Glacier National Park, Montana.

Year	Kill Rate	hunter -days/ deer	hunter -days/ elk	days > 30 cm snow	Prop. deer	Prop. elk	# of wolves	bout length (km)
1986	na	12.6	34.9	57	0.43	0.57	na	na
1987	14.8	19.9	38.9	76	0.49	0.49	8	503
1988	41.7	27.8	73.9	5	0.56	0.45	7	292
1989	11.6	22.7	73.5	85	0.86	0.14	10	405
1990	17.3	27.7	151.1	69	0.79	0.21	6	207
1991	6.8	19.7	82.7	104	0.82	0.19	18	381
1992	11.4	24.4	85.8	13	0.70	0.23	19	193
1993	3.4	28.6	228.6	105	0.91	0.05	25	54
1994	8.2	38.5	113.3	70	0.89	0.11	29	303
1995	11.9	24.9	107.2	74	0.77	0.23	24	298
1996	na	55.8	260.2	30	0.73	0.20	na	

Table 2. Species of prey selected by wolves to encounter and kill in and near Glacier National Park, 1992-96.

		Killed by Wolf		Systematic		Wolf Travel	
Wolf Pack	Species	Prop.	n	Prop.	tracks /km	Prop.	tracks /km
Camas							
	White-tailed deer	0.826	(138)	0.744	(14.8)	0.890	(23.5)
	Elk	0.137	(23)	0.161	(3.2)	0.091	(2.4)
	Moose	0.029	(5)	0.096	(1.9)	0.019	(0.5)
Spruce							
	White-tailed deer	0.043	(1)			0.073	(0.3)
	Elk	0.348	(8)			0.317	(1.3)
	Moose	0.609	(14)			0.610	(2.5)

Factors Affecting Selection

When all the kills made by cougars and wolves from 1986-1996 were compared, there was no difference among the mean femur marrow fat (FMF) of deer (71.4, n = 244), elk (71.1, n = 76), or moose (64.6, n = 32; F = 2.12; df = 2, 299; P = 0.122). Results were similar when marrows from males and females were analyzed separately. There was no difference among deer, elk, and moose in the percentage of fawn/calves (34.1, 35.4, 41.0, respectively), prime (59.0, 54.9, 48.7) and old age categories (6.9, 9.7, 10.3, respectively) killed by wolves and cougars (χ = 2.39, 4 df, P = 0.664). Additionally, there was no difference among deer, elk, and moose in the percentage of males (51.3, 46.3, 63.0, respectively) killed by wolves and cougars (χ = 2.27, 2 df, P = 0.321). These trends remained when cougar kills were excluded from this analysis.

Over the entire study area a greater proportion of moose than deer were killed in March (χ = 11.10, 4 df, P = 0.025; Table 3). In Camas territories, a greater proportion of elk than deer were killed in March (χ = 6.17, 2 df P = 0.05; Table 3).

The proportion of deer selected by wolves was

Table 3. Proportion of deer, elk and moose killed by wolves and cougars during winter months in and near Glacier National Park, 1986-1996.

Month	deer	elk	moose
All Packs			
January	0.349	0.182	0.133
February	0.437	0.386	0.467
March	0.214[a]	0.432	0.400[a]
Camas Packs			
January	0.344	0.179	
February	0.440	0.393	
March	0.216[b]	0.429[b]	

[a] Significant difference between pair (P = 0.003)
[b] Significant difference between pair (P = 0.02)

correlated with number of wolves ($r = 0.669$, $P = 0.025$; Table 1), year ($r = 0.676$, $P = 0.022$), and marginally with hunter-days/elk harvested ($r = 0.547$, $P = 0.082$). When all independent variables were examined simultaneously, the number of days with > 30 cm snow was the only independent variable that was significantly correlated with proportion of deer selected by wolves from 1986-96 ($r = 0.79$, $P = 0.02$). Proportion of elk selected by wolves was negatively correlated with number of wolves ($r = -0.715$, $P = 0.013$), year ($r = -0.733$, $P = 0.010$), and hunter-days/elk harvested ($r = -0.624$, $P = 0.040$; Table 1). When all independent variables were examined simultaneously, no variable was significantly correlated with the proportion of elk selected by wolves.

Rate of encounter of elk tracks along wolf routes did not change from 1990-95 (Kruskal-Wallis $\chi^2 = 6.72$, 6 df, 0.132; Table 4). Rate of encounter of deer tracks increased from 1991 to 1992 (Mann-Whitney U $Z = -2.34$, $P = 0.019$; Table 4) and from 91 to 94 (Mann-Whitney U $Z = -4.25$, $P < 0.0001$).

Kill Rate

Yearly mean kill rate for all packs combined ranged from 3.4 km/kill in 1993 to 41.7 km/kill in 1988 (Table 1). Total wolf kill rate (1/[km/kill] = kills/km) was correlated with days having > 30 cm snow on the ground ($r = 0.731$, $P =$

Table 4. Encounter rates of deer, elk, and moose along wolf hunting routes in Camas territories, 1990-1996 in and near Glacier National Park, Montana.

	deer tracks/km		elk tracks/km		moose tracks/km	
Year	med	sd	med	sd	med	sd
1990	1.2	32.1	0.0	3.4	0.0	0.3
	11.1[1]	29[2]	1.9	29	0.0	29
1991	0.7	26.9	0.0	4.3	0.0	0.8
	11.8	89	1.4	89	0.6	89
1992	3.0	65.0	0.0	14.8	0.0	14.6
	28.5	73	2.8	73	2.1	73
1993	1.1	79.9	0.0	17.0	0.0	2.6
	24.6	97	3.0	97	0.6	97
1994	6.0	71.8	0.0	19.1	0.0	1.9
	38.1	291	3.4	291	0.3	291
1995	0.7	63.1	0.0	6.7	0.0	2.5
	20.7	75	2.4	75	0.6	75

---

[1] mean

[2] n

0.025) and with proportion of deer selected by wolves (r = 0.655, P = 0.055). Only the number of days with > 30 cm of snow on the ground entered the multiple regression of variables correlated with total wolf kill rate. When controlling for the other variables, there was a marginally significant positive linear relationship between total wolf kill rate and total number of wolves (r = 0.623, P = 0.099) and when this was added to the regression model the multiple correlation coefficient improved to 0.85. Kill rate per wolf was marginally correlated with days with > 30 cm snow on the ground (r = 0.615, P = 0.078), and marginally with proportion of deer selected (r = 0.617, P = 0.076). Only proportion of deer selected entered the multiple regression of variables correlated with kill rate per wolf. There was a marginally significant positive linear relationship between kill rate per wolf and year (r = 0.66 P = 0.057). The relationship was highly significant when an exponential curve was fit to the data (r = 0.78, P = 0.013). Kill rate per wolf was related to hunter-days/elk in an exponential fashion (r = 0.70, P = 0.035) but not hunter-days/deer (r = 0.40, P = 0.283).

Total wolf deer kill rate was marginally correlated with wolf density (r = 0.583, P = 0.099), year (r = 0.588, P = 0.096), and with days with < 30 cm snow on the ground (r = 0.726, P = 0.027). Days with > 30 cm snow on the ground (P = 0.038) and number of wolves (P = 0.085) entered the multiple regression of variables correlated with total wolf deer kill rate ($\underline{r}$ = 0.85). Total wolf elk kill rate was marginally correlated with days with > 30 cm snow on the ground ($\underline{r}$ = 0.65, $\underline{P}$ = 0.058). Only days with > 30 cm snow on the ground entered the multiple regression of variables correlated with total wolf elk kill rate.

Hunting Pattern

Deer ($\bar{x}$ = 33.0 tracks/km, med = 4.0, SD = 67.0 $\underline{n}$ = 100) and elk density ($\bar{x}$ = 6.0, med = 0, SD = 29.0 n = 101) was significantly lower in areas where wolves hunted in a dispersed mode versus areas where they hunted in a concentrated fashion (deer: $\bar{x}$ = 45.0 tracks/km, med = 9.0, SD = 72, $\underline{n}$ = 93; MW $\underline{Z}$ = - 2.20, $\underline{P}$ = 0.028, elk: $\bar{x}$ = 1.0, med = 0.0, SD = 4.0 $\underline{n}$ = 93; MWU $\underline{Z}$ = -1.83, $\underline{P}$ = 0.067). There was no difference in moose density between these areas (dispersed: $\bar{x}$ = 0.0, med = 0.0, SD = 1.0, $\underline{n}$ = 101, concentrated: $\bar{x}$ = 0.0, med = 0.0, SD = 3.0, $\underline{n}$ = 93; MW $\underline{Z}$ = -1.19, $\underline{P}$ = 0.235).

Home Range Use

South Camas wolves shifted spatial use patterns significantly between 1993 ($\underline{n}$ = 29 locations) and 1994 ($\underline{n}$ = 33 locations; MRPP $\underline{P}$ = 0.0035). Likewise, dispersion of kills shifted from 1993 ($\underline{n}$ = 50) to 1994 ($\underline{n}$ = 29; MRPP $\underline{P}$ = 0.00005). Home range size and kill dispersion area size increased from 1993 (6,283 ha, 1,509 ha, respectively) to 1994 (15,490 ha, 5,527 ha, respectively). This shift resulted from a reduction of hunting in the Camas winter range (Fig. 2, chpt 1) and an increase in hunting in the Bowman winter range and from an increase of forays north into North Camas territory. Mean number of deer pellets/plot declined significantly from 1993 (0.641, SD = 1.32) to 1994 (0.193, SD = 0.465; Mann-Whitney $\underline{Z} = -2.63$, $\underline{P} = 0.009$) in the Camas winter range. There was no change in mean number of pellets/plot from 1993 (1.40, SD = 1.65) to 1994 (1.29, SD = 1.38; Mann-Whitney $\underline{Z} = -0.002$, $\underline{P} = 0.99$) in the Bowman winter range. Spatial use pattern did not differ between 1994 and 1995 $\underline{n} = 50$; MRPP $\underline{P} = 0.293$) nor did dispersion of kills ($\underline{n} = 13$; MRPP $\underline{P} = 0.22$), but home range size and kill dispersion area size declined in 1995 (8,454 ha, 5,295 ha, respectively).

North Camas wolves shifted spatial use patterns significantly between 1993 ($\underline{n} = 22$ locations) and 1994 ($\underline{n} = 26$ locations; MRPP $\underline{P} = 0.001$). Likewise, dispersion of kills shifted from 1993 ($\underline{n} = 20$) to 1994 ($\underline{n} = 26$; MRPP $\underline{P} = 0.0024$). Home range size and kill dispersion area size was smaller in 1994 (9,431 ha) than in 1993 (14,420 ha), but kill dispersion area size was larger in 1994 (11,460 ha) than in 1993 (2,900 ha). This shift north resulted from a reduction in use of southern portions of their territory (adjacent to South Camas territory) and from a reduction of hunting in the Upper Kintla winter range. Spatial use pattern did not differ between 1994 and 1995 ($\underline{n}$ = 28; MRPP $\underline{P}$ = 0.149) nor did dispersion of kills ($\underline{n}$ = 11; MRPP $\underline{P}$ = 0.10), but the sizes of their home range and kill dispersion areas were smaller (7,991 ha, 3,287 ha, respectively).

Spruce pack spatial use patterns did not differ between 1993 ($\underline{n}$ = 19) and 1994 ($\underline{n}$ = 17; $\underline{P}$ = 1.00) or between 1994 and 1995 ($\underline{n}$ = 16; $\underline{P}$ = 0.161). Sample size of kills was too small to analyze.

DISCUSSION

Whether wolves have a preferred or optimal prey species in multi-prey environments in North America has been a subject of debate (Carbyn 1983, Weaver 1994). A preference would affect wolf behavior and habitat choice at several scales and may be the ultimate factor affecting these. On a regional scale, wolves initially may be more likely to colonize areas with an abundance of their preferred prey. Distribution of the preferred prey within a given drainage may then affect where wolves establish home ranges in that drainage and affect wolf use and movements within that home range (Singleton 1995, chapter 3). Alternately, no particular prey species may be optimal and landscape and habitat factors and distribution and abundance of prey species would drive selection of prey by wolves. These "external" factors driving selection also occur at several scales (Huggard 1993<u>a</u>, Weaver 1994, chapter 3).

Wolves in the North Fork (NF) selected areas for travel with greater densities of deer and lower densities of elk; these were primarily white-tailed deer winter yards. For example, the South Camas Pack was present in the Logging yard for 49% of the days they were monitored (chapter 5) and Singleton (1995) indicated this relatively small part of their home range received the heaviest use. Deer used these yards consistently and predictably each year (Rachael 1992, K. Kunkel, unpubl. data), although densities varied by winter severity (chapter 3). As a result, wintering areas provide consistently high prey encounter rates for wolves. White-tailed deer habitat use during winter is more influenced by snow depth than is elk or moose habitat use (Telfer and Kelsall 1984, Jenkins and Wright 1988). White-tailed deer concentrate in areas with habitat and physical features that reduce snow depths. They concentrate at relatively high densities to maximize anti-predator benefits (Nelson and Mech 1981, Messier and Barrette 1985, chapter 3). Use of these areas is traditional and thus very predictable. Predators can maximize foraging efficiency by concentrating their hunting in these yards. Because elk and moose are less restricted by snow depths, they are more dispersed, more mobile, and can remain in a wider and less predictable array of habitats (Jenkins and Wright 1988, Bureau 1992, Langley 1993, K. Kunkel, unpubl. data). More time and energy is required by predators to locate these patches of prey. Similarly Huggard (1993a) found that in Alberta herds of elk were predictably located and wolves spent a disproportionate amount of time in these areas, whereas mule deer (Odocoileus hemionus) were found in small groups and were not predictably associated with one location.

Wolves selected to kill elk and moose over deer within the deer yards. This appears to be best explained in terms of profitability. Following Huggard (1993a), profitability equals the ratio of net energy gain to handling time (e/h). Huggard (1993a) broke h into 4 components: chase time, time to kill the animal once it is caught, time to eat the meat, and time to digest and argued that based on track evidence the first 3 were relatively short (due to complex mountain topography) and were generally equal for elk, deer, and sheep. He further argued that because of this and because time to digest was proportional to size of prey, the ratio of e/h differs little between these ungulate species. Therefore, all or none should be attacked or tested upon encounter. We agree with Huggard's (1993a) breakdown of the 4 components of handling he listed. Our comparison of prey condition of deer, elk, and moose indicated similar vulnerability of each species to wolves. A greater proportion of poorer condition individuals of a given species would indicate reduced vulnerability of that species (Temple 1987). We know of no published study that has made a similar direct comparison of cervid vulnerability to predation. These results may still be considered tenuous, however, because we could not estimate marrow fat levels or the age distribution in each cervid population at large. Selection for moose in poorer condition may have been occurring if, for example, the mean marrow fat in moose available was greater than the mean marrow fat in deer available.

Contrary to these findings, year-round survival rates of radio-tagged deer in our study area were lower than those for elk which were lower than those for moose, possibly indicating greater year-round vulnerability of deer to predators (chapter 2). Additionally, selection for deer increased with greater snow depths indicating that this factor may cause deer at times to become more vulnerable than elk or moose. Mech et al. (1995) found a similar phenomenon in a wolf, caribou (Rangifer tarandus), and moose system. A major increase in selection for caribou and against moose occurred during above-average snowfall winters. Potvin et al. (1988) reported that selection of deer decreased and selection for moose increased during mild winters. They speculated that reduced snow depths may make moose easier to capture than deer because deer are faster in this circumstance.

Two additional factors may affect selection. First, risk of injury may affect whether wolves decide to attack an animal or not. Huggard (1993a) believed that of deer, elk, and moose, only moose posed a significant enough risk to affect the attack decision of wolves. The risk posed by moose in our study area apparently wasn't significant enough to dissuade wolves because moose were selected over deer. Second, the probability of capture after attack will affect observed selectivity if success of capture differs among prey species (Nishimura and Abe 1988). No published studies directly compare relative rates of capture success by wolves for deer, elk, and moose. Success rates are low for moose (Mech 1966a, Haber 1977, Peterson 1977) and deer (Nelson and Mech 1993, but see Kolenosky 1972). Some researchers have argued that smaller ungulates (deer and caribou) should be easier to capture than larger ungulates, and evidence cited for this is that the smaller prey is usually predominant in the diet when larger prey is also available (Mech and Frenzel 1971, Carbyn 1974, Haber 1977, Mech 1977a, Carbyn 1983, Potvin et al. 1988, Forbes and Theberge 1996). Potvin et al. (1988) reported that even when deer were near local extinction, wolves persisted in hunting the few remaining individuals while moose were a small fraction of the diet. We believe that the smaller-is-easier theory is often too simplistic and that many other variables probably more importantly affect capture success (Skogland 1991, chapter 3). While we have no data that directly compares relative success rates of capture among deer, elk, and moose, the lack of difference in condition among deer, elk, and moose killed by wolves and cougars indicates similar rates of success for attack on each of these species. We therefore believe selectivity for elk and moose did not result from variable success rates. We believe selection for elk and to a lesser degree for moose over deer upon encounter results from the fact that they are indeed more profitable than deer.

We believe that when measuring handling time, Huggard (1993a) should have included search time as a component (Weaver 1994). Elk have approximately 3 times the biomass of deer and thus provide 3 times as many meals for wolves. Elk should be selected because they provide more meals per unit of search effort (assuming similar search time for deer and elk). The time required by wolves to search for a vulnerable prey animal is greater than any other component affecting kill rate (Mech 1992). Three successful hunts for deer are required to equal one successful hunt of an elk.

Huggard (1993a) further broke down his analysis to compare selection based on individual versus herd encounter rates and found that based on per herd encounters, deer were underrepresented in the diet of wolves. He provided evidence that a herd of elk responds to wolves as a single unit. We agree that this analysis makes good biological sense, however, we believe that the same notion applies to white-tailed deer in our study area. White-tailed deer were present in relatively dense concentrations in deer yards, and a portion of those deer responded to wolves as a unit. Similar to Huggard's (1993a) finding for elk, groups of deer flee together from a threat (K. Kunkel, pers. obs. and unpubl. data) and, probably because of increased wariness following this, consecutive kills of deer are probably rarely made from the same group (chapter 5). Group sizes of deer are variable and difficult to quantify but are probably at least the size of most elk groups in our study area. For this reason, we did not attempt to define encounters on a per herd/group basis. Had we done such an analysis, selection for moose would have declined relative to deer and elk. More research is needed on this subject.

Based upon review of 9 studies of prey selection by wolves in multi-prey environments, Weaver (1994) postulated that wolf selection for deer appeared to be inversely related to vulnerability of elk. On a per elk basis, elk are less vulnerable to wolf predation in larger groups in more open habitat (see above). Elk, however, are more vulnerable in smaller groups in wooded habitats (Huggard 1993a, Weaver 1994). The latter describes elk behavior for much of the winter in our study area, especially in more severe winters (Bureau 1992, K. Kunkel, unpubl. data).

Selection occurs at several levels and we believe the most important level ultimately affecting selection overall is selection for encounter (deer in our study area). Where wolves select to travel and encounter prey is the most influential element on what finally ends up being consumed (Scheel 1993). Once hunting areas are selected the actions that follow are opportunistic. Wolves will likely in some way test every prey they encounter but may be more persistent in testing elk and moose because they are more profitable prey. At this level success rates will have the most influence on selection.

The best estimate of availability in wolf prey selection studies (including ours) has been based on ungulate tracks encountered along wolf tracks. While this indicates relative spatial overlap of wolves and prey it does not estimate temporal overlap. We do not know what prey were actually encountered by wolves. The real value may be different from estimates based on tracks. Only by directly observing wolves hunting prey can we estimate true encounter and capture rates. We suspect that similar to other large carnivores, wolves are primarily opportunistic hunters upon encounter, and that most selectivity is generated by choice of travel routes or hunting areas (Scheel 1993).

Of the factors we examined, only snow depth was correlated with proportion of deer in wolf diets; as snow depth increased, selection for deer increased. Based on his analysis of prey selection, Huggard (1993a) hypothesized that changes in density of a particular prey species would have the greatest influence on wolf diet. We found no significant correlation between proportion of deer selected and abundance of deer, but did find a weak, significant negative correlation with the abundance of elk. Prior to 1989, elk and deer comprised similar proportions of wolves' diets. While we have no estimates of relative availability for that time period, Jenkins (1985) estimated that based on track counts, deer and elk populations were roughly equal along the river bottom portion of our study area during 1982 and 1983. Elk:deer ratio has subsequently declined, and deer have become the dominant prey item selected by wolves.

Kill Rates

Our methods did not allow us to estimate kill rates per unit time but only kill rates per kilometer traveled by wolves. For this reason, we cannot estimate the actual number of prey killed per winter. Had we estimated the mean distance traveled by wolves per day, we could have obtained an estimate of total kill. We believe that this is probably too great of an extrapolation. We can, however, make relative comparisons with other studies. The annual kill rate of wolves in our study area varied 12 fold, similar to the 15 fold variance found in Isle Royale wolves (2.5-43.0 days per kill per pack; Thurber and Peterson 1993). Wolves on Isle Royale travelled an average of 14.3 km/day (Mech 1966a). During a severe winter, the kill rate of deer by wolves in northeastern Minnesota varied 6 fold (6.3-37.5 days/kill/wolf; Mech and Frenzel 1971). Daily distances traveled by a pack of 8 wolves during one winter in Ontario ranged from 0.0-21.2 km and averaged 7.1 km (Kolenosky 1972). The distance travelled between kills varied from 0.3-43.4 km (almost identical to our range) and averaged 14.7 km, they killed one deer every 2.2 days with a maximum kill rate of 8 deer in 8 days and a minimum kill rate of one deer per 4.2 days.

Information on factors affecting wolf predation rates including the role of prey density is very limited. We found a significant negative correlation between kill rate per wolf and elk density (as indexed by hunter-days/elk). Kill rate increased as elk density decreased. Kill rate, however, was not significantly correlated with deer density and the kill rate of elk was not significantly correlated with elk density. The elk population has probably declined more than the deer population, but both have declined significantly since wolves recolonized the North Fork (chapter 2). These population trends have been negatively correlated with wolf density, although grizzly bear (Ursus arctos) and cougar (Puma concolor) populations increased concurrently with wolves. We have estimated the relative role of these predators in the prey declines by analyzing cause-specific mortality rates of radio-tagged deer, elk, and moose (chapter 2). An increase in predation rate with a decrease in prey density indicates a destabilizing "antiregulatory" effect (Lidicker 1978) of wolf predation and indicates a predator that is highly efficient in capturing prey at low densities. Wolves have been ascribed this characteristic in Quebec where they "hunted harder" when prey densities declined (Potvin et al. 1988). Messier (1995) described this as a type 2 functional response (sensu Holling 1959) where the kill rate climbs quickly to a plateau where it is then strongly depensatory (Messier 1995). Messier (1994) reported that a type 2 functional response best fit moose and wolf systems, and Dale et al. (1995) reported a type 2 response for wolves preying on caribou in a multi-prey system. The availability of alternate prey in the North Fork may allow wolves to maintain heavy predation pressure on a low density prey species.

An antiregulatory or depensatory effect, or at least a loose regulatory feedback effect, has been reported for wolves and deer in Quebec (Potvin et al. 1988) and Minnesota (Mech 1977b) and wolves and moose in Alaska (Gasaway et al. 1983) and on Isle Royale (Peterson and Page 1988). The availability of alternate prey, or increase in hunting effort of wolves may have produced a lag effect in the decline in the wolf population (Gasaway et al. 1983, Potvin et al. 1988). The wolf population decline has only recently begun in the North Fork (see below). Ten years after the local disappearance of deer in the Quebec study area, they returned to "fairly abundant" levels (Potvin et al. 1988) following a decline in wolf numbers, a series of mild winters, and strict harvest regulations. A similar phenomenon has occurred in northern Minnesota (L.D. Mech, U.S. Geological Survey, pers. comm.) and is occurring in Ontario (Forbes and Theberge 1996) and on Vancouver Island (Hatter and Janz 1994). The high reproductive rate of white-tailed deer and their well-developed anti-predator strategies (Nelson and Mech 1981, Gasaway et al. 1983, chapter 3) make them very resilient in these systems.

Where they coexist in the northern U.S. and Canada and have been well-studied, wolf and deer (Odocoileus spp.) populations have been unstable for the duration they have been examined (the last 20-40 years; citations in Potvin et al. 1988, Fuller 1990, Hatter and Janz 1994). Skogland (1991) believed that the dynamics of northern ungulates and their predators appeared to be similar to rodent-driven cycles of small mammal systems. Additional factors that interact with wolf predation to generate this instability include winter severity, hunting pressure, and large scale habitat modifications (Mech and Karns 1977, Potvin et al. 1988, Hatter and Janz 1994, Forbes and Theberge 1996). The precise role of wolf predation in this mix is still debated, but is no doubt significant. The density and diversity of predators in our study area included black (Ursus americanus) and grizzly bears where almost no regulatory feedback might be expected because they are not obligate predators. This may result in a much slower recovery rate of prey than in other systems. Given the large-scale, density-independent disturbances and loose regulatory feedback inherent to these northern systems, we don't think this instability is surprising (Peek 1980, Botkin 1990).

Factors Affecting Kill Rate

The number of days with > 30 cm snow and wolf density best explained the variation in total wolf kill rate in our study area. The enhanced vulnerability of prey to wolves created by deep snow has been reported in numerous studies (Mech and Frenzel 1971, Mech and Karns 1977, Peterson 1977, Nelson and Mech 1986, Fuller 1991, Boyd et al. 1994, Mech et al. 1995). However, Fuller (1989) and Dale et al. (1995) found no correlation between snow depth and wolf kill rate of deer or caribou. Other than our study, only Huggard (1993b) found a significant relation between wolf kill rate (of primarily elk) and snow depth. Fuller (1991) suspected that the discrepancy between increased prey mortality rates in deep snow and the lack of change in wolf kill rates resulted from the reliance of many studies examining wolf kill rates upon location of kills from the air. This technique is known to be sensitive to the time wolves remained at kills. Only Huggard (1993b), Dale et al.

(1995), and our study followed wolf tracks to locate kills. Dale et al. believed that snow depth may not have had an effect on kill rate because wolves were at or near food satiation in most cases in their study. Huggard (1993b) believed that increased snow depths increased encounter rates with prey and this was the mechanism most responsible for increasing kill rates. We believe that the reduced access to food for deer caused by deep snow and their subsequent poor condition was the major factor responsible for increased predation rates (chapter 3). The correlation between total wolf deer kill rate and snow depth was significant while the correlation between total wolf elk kill rate and snow depth was only marginally so.

The correlation between wolf density and total kill rate may seem intuitively likely, however, Peterson and Page (1987) found no such correlation on Isle Royale and suggested that accurate predictions of wolf kill rates based on wolf density cannot be made probably because of the wide range of functional response in wolves. Abrams (1993) argued that the assumption of a linear relation between the death rate of prey and predator density is too simplistic. He argued that adaptive antipredator behavior greatly reduces this likelihood. Although we agree with this and provide evidence for it (chapter 5), we believe that wolf density may be used by mangers to predict overall predation rates for recolonizing wolves in the Rockies.

Wolf density and total wolf deer kill rate was significantly correlated but wolf density and total wolf elk kill rate was not. We know of no other published study that has reported kill rates per prey species in multi-prey systems and we know of no other published study that has shown a correlation between wolf density and kill rate. However, other researchers have reported a positive relationship between pack size and kill rate (Messier and Crete 1985, Ballard et al. 1987, Sumanik 1987, Thurber and Peterson 1993, Dale et al. 1995). These researchers speculated that larger packs had reduced handling and search times and higher energy demand compared to smaller packs. Similar to Haber (1977) and Hayes et al. (1991), we found no relationship between pack size and predation rates. Even small packs can kill moose (Thurber and Peterson 1993) so it is not too surprising that smaller packs would have kill rates on deer similar to large packs. Thurber and Peterson (1993) also speculated that smaller packs may have higher rates of kill due to greater losses to scavengers; the wide diversity and density of scavengers in our study area certainly makes this possible. Additionally, Thurber and Peterson (1993) speculated that kill rates may not reflect pack size because of the predominant influence of alpha wolves.

In our study, the proportion of deer in the diet accounted for most of the variation in kill rate per wolf.

We believe this reflects the lower biomass of food provided by deer versus elk and moose and results in wolves spending less time feeding at deer kills. However, contrary to our earlier statements, this could also be interpreted as a reflection of the ease of killing deer versus elk and moose. We believe the former interpretation is more sound because deer selection affected kill rate per wolf and not total kill rate. Dale et al. (1995) found that the amount of food available from a kill was a significant factor in explaining the length of the interval until the next kill.

Effects of alternate prey on kill rates have not been previously examined. Messier (1995) speculated that in multi-prey systems where one prey is especially more vulnerable, prey switching may cause the functional response to be sigmoid (type 3) in the less vulnerable species. We found no evidence (outside of heavy snow winters) to indicate that deer were more vulnerable than elk to predation by wolves (and vice versa, but see chapter 2), and wolves apparently exhibited a type 2 response to both species.

Hunting Pattern

Wolves have been reported to travel in single file through deep snow in areas devoid of deer, and to fan out into groups of 2 or 3 or singly in areas where deer were present (Stenlund 1955, Kolenosky 1972). The purpose of this behavior was ostensibly to locate or flush deer although the confounding effects of snow depth weren't discussed. Mech (1966b) and Huggard (1993a) did not see wolves exhibit this behavior. Our tracking indicated that wolves "fanned out" in areas of lower deer density. We speculate this behavior may improve searching efficiency by wolves in areas of sparse prey.

Use of Space

Wolves modified their use of space rapidly and relatively dramatically apparently in response to local changes in prey abundance. This undoubtedly increased their searching and killing efficiency of prey and may have resulted in an antiregulatory response to overall prey density. Territory use by Camas wolf packs was very dynamic between 1993 and 1995. Numbers and sizes of packs in the North Fork have fluctuated greatly since the onset of recolonization by wolves (Ream et al. 1991). This scenario should be expected in the early years of recolonization (Fritts and Mech 1981, Peterson et al. 1984) and may also occur in heavily harvested wolf populations (Ballard et al. 1987), naturally-regulated wolf populations (Meier et al. 1995), and where prey is significantly declining (Mech 1977a). We believe the latter situation portrays the current dynamics of wolf space use in the North Fork. The South Camas pack reduced their use of the Camas deer winter range probably because of a significant reduction in deer using that winter range (resulting from differences in winter severity and population decline). They then expanded their territory north and began trespassing into the North Camas pack territory, and at least 4 wolves were killed by other wolves as a result of this (Pletscher et al. 1997, K. Kunkel, unpubl. data). These incursions resulted in a reduction of the territory size of the North Camas pack. Expansions in territory size have been reported for coyotes (Canis latrans) during food shortages (Mills and Knowlton 1991). Forbes and Theberge (1996) reported that wolves began excursions to a deer yard outside their territory when density of deer within their territory fell below $0.02/km^2$. Messier (1985) found that moose densities below $0.2/km^2$ caused wolves to change territory boundaries, increase extraterritorial excursions to deer areas, and become more susceptible to mortality. As deer became locally extirpated in Minnesota, wolves trespassed more, selected more moose, and foraging time and pup survival decreased (Mech 1977b).

MANAGEMENT IMPLICATIONS

We believe that wolves recolonizing multi-cervid systems in areas of the Rocky Mountains where snow is a dominant influence will select areas with the highest densities of white-tailed deer because of their predictable use of wintering areas. Gross analysis from Montana indicates such selection has occurred; 8 of 9 packs were established in areas where the most abundant prey is deer (K. Kunkel pers. obs., J. Fontaine, U.S. Fish and Wildl. Serv., pers. commun.). Dale et al. (1995) determined that species of prey explained significantly more variation in wolf density than total ungulate biomass alone. Based on this, managers may be able to predict on a regional scale what areas wolves will first recolonize and where wolf densities will be greatest. Prey in these areas should be monitored carefully.

Wildlife managers and the public should expect significant declines in some prey populations with wolf recovery in the Rockies, and some of these declines may be relatively long-lasting. Declines may be anticipated in deer populations, and selection for deer may increase during and following severe winters. Kill rates on deer will be relatively higher than kill rates on elk and moose (chapter 2), and kill rates may increase with wolf density and may remain high even after significant declines in the prey population. The management recommendations of Gasaway et al. (1983) remain sound if relatively quick recovery of prey or higher densities of prey are desired. Predation levels should be reduced as quickly as possible where these are the primary factors responsible for the decline and where these options are possible and acceptable. We recommend male-only harvests, winter range habitat enhancement, alternate prey enhancement, and increased harvests levels for predators that are hunted (cougars in our study area; chapters 1, 2, 3, and 5). As stated by Gasaway et al. (1983:38), "the long-term consequence of procrastination by managers will likely be a scarcity of primary and alternate prey as well as predators for many years." This notion is especially important to consider in areas where predators are classed as threatened or endangered. We recommend that prey populations be monitored intensively where wolves are recolonizing in the Rockies so that conservative harvest regiments can be incorporated in quick response to prey declines, before these declines become problematic. More aggressive measures can be taken if serious predator-caused declines continue, including those outlined above and elsewhere (Boertje et al. 1995). We advise managers to ask the questions outlined in the chart developed by Theberge and Gauthier (1985:456) before proceeding with predator management options and believe these should be incorporated along with management options and predator and prey population objectives into state predator/prey management plans. Further, management agencies and the public should be prepared for the dramatic changes that occasionally occur in predators and their prey (Gasaway et al. 1983). Finally, we agree with Van Ballenberghe and Ballard (1994) that questions of prey limitation and regulation by predators should focus on conditions leading to such states, rather than debating whether they occur.

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CHAPTER 5: EFFECTS OF WOLVES ON BEHAVIOR OF WHITE-TAILED DEER IN GLACIER NATIONAL PARK

Abstract: We examined the effects of the presence and absence of wolves (Canis lupus) in a white-tailed deer (Odocoileus virginianus) winter yard on deer movements and habitat use by simultaneously locating wolves and deer. We tested the relative risk of predation in different habitats within the yard by comparing the feeding effort ("giving-up-density") of deer at sites with dense stalking cover versus sites with sparse stalking cover. Wolves were present in the yard on 40% of the days they were monitored. Five of 10 radiocollared deer made significant shifts in distribution in the presence of wolves. There was no difference in sizes of deer home ranges in the presence or absence of wolves. In the presence of wolves, deer used areas with denser canopy cover than they did in the absence of wolves. Deer used canopy cover class patches that were smaller in area and deer were closer to edges of these patches in the presence versus the absence of wolves. Giving-up-density was higher at sites with dense stalking cover indicating that these areas may have higher predation risks for deer. White-tailed deer in winter yards reduced risk of predation at 2 levels. First, they reduce the encounter and detection rates of wolves by shifting away from wolf use areas and also by concurrently moving into denser hiding cover.

Secondly, deer reduce wolf capture rates by using areas with low levels of stalking cover. This increases their likelihood of detecting predators and subsequently improves their chance for escape. The continued presence of wolves in a yard apparently "depresses" the availability of deer to wolves and, as a result, wolves move to a different yard to improve their foraging efficiency. Predator/prey managers should conduct experiments to determine if deer survival is enhanced by maximizing concentrations of deer in a few yards and manipulating the juxtaposition of maximum hiding cover and minimum stalking cover therein.

INTRODUCTION

Most studies of predator-prey relationships in large mammals have focused on the direct lethal effects of predators on the population dynamics of their prey (Mech and Karns 1977, Gasaway et al. 1983, Messier and Crete 1985, Peterson et al. 1984, Bergerud and Elliot 1986, Ballard et al. 1987, others). The effects of predation, however, go far beyond direct mortality. The risk of predation affects foraging, vigilance, patch use, diet, reproductive behavior, and parental care of prey (review in Lima and Dill 1990, Sinclair and Arcese 1995). Few decisions an animal makes are as critical as predator avoidance. As a result, it has been argued that almost all behavior and habitat use should be viewed as avoidance of predation (Lima and Dill 1990). Until recently, most studies of habitat preferences of cervids have ignored this (c.f. Keay and Peek 1980, Jenkins and Wright 1988, Pauley et al. 1993, others, but see McNay and Voller 1995 for black-tailed deer [Odocoileus hemionus]). Relatively few studies have examined the effects of predators on cervid foraging, movements, distribution, and habitat selection (Bergerud et al 1984, Edwards 1983, Bergerud et al. 1984, Stephens and Peterson 1984, Bergerud 1985, Bergerud and Page 1987, Ferguson et al 1988, Risenhoover and Bailey 1985, Berger 1991, Sinclair and Arcese 1995).

One way prey may respond to the presence of predators is by shifting activity to less risky microhabitats (Brown et al. 1988, Werner et al. 1983, Edwards 1983, Lima et al. 1985, citations above). Prey may seek "cover" when predators are present to: 1) reduce the chance of encounter with a predator (Watts 1991), 2) reduce the chance of detection by a predator, or 3) reduce the probability of capture by a predator (Bergerud and Page 1987).

White-tailed deer (Odocoileus virginianus) escape predation from wolves (Canis lupus) by relying on individual and group alertness and short bursts of speed to escape predation by wolves (Mech 1970, Mech 1984, Lingle 1992). The ability of deer to use such a strategy may be limited in certain habitats on their winter range (ie. habitat with low visibility; chapter 3). Alternatively, particular habitats in a deer's home range may offer refuge from predation

(Dasmann and Taber 1956:155, Sweeney et al. 1971). The characteristics and survival value of these areas are unknown. Very little information on deer exists regarding possible anti-predator strategies associated with habitat selection (Hirth 1977, Nelson and Mech 1981). Knowledge of habitats important to deer for escaping predation may provide information on how to manipulate winter ranges to favor survival of deer (when this is deemed necessary) in the face of predation.

Changes in behavior associated with the presence of a predator may limit foraging efficiency of cervids (Edwards 1983, Klein 1985, Berger 1991, Kotler et al. 1994). This may result in reductions in a given animals's nutritional condition which in turn may affect its susceptibility to predation (Hik 1995). Hornocker (1970:35) believed that the presence of cougars (Puma concolor) kept "ungulates moving on their winter ranges" and may have forced them to abandon use of certain areas. Presence of cougars has forced abandonment of winter range by bighorn sheep (Ovis canadensis) in California which has resulted in sheep in poor condition and population declines (Wehausen 1996). Determination of the effect of wolf presence on deer behavior may provide data for further refinement of our predictions of the effects of predation on cervids.

Previously, we found a correlation between wolf and cougar hunting success and density of stalking cover (chapter 3). Herein we test the null hypothesis of no difference in deer vulnerability to predation in habitats with dense vs sparse stalking cover by comparing "giving-up-density" in deer in these habitats. If risk of predation increases costs of foraging, animals will balance this cost by leaving a patch at a higher giving-up-density (Kotler et al. 1994). Giving-up-density may be defined as the amount of food remaining in a patch at the point the consumer moves to another patch to forage. Determining the predatory risk of habitats will provide managers information on how to manipulate winter ranges to increase security of deer in the face of predators.

We studied wolves and white-tailed deer in Glacier National Park from 1990 through 1996 to determine the effect of wolf presence on white-tailed deer habitat use, movements, and home range size and to determine which habitats offer the most security from predation.

STUDY AREA

This study was conducted in the Logging Creek Winter Range (LWR; Fig. 2, chpt. 1; Fig. 1) in northwestern Glacier National Park, Montana. This winter range lies primarily on a gentle southwest facing slope and along the river bottom of the North Fork of the Flathead River. Cottonwood (*Populus trichocarpa*)/lowland spruce (*Picea engelmanii*) communities dominate the river bottom and Douglas-fir (*Pseudotsuga menziessi*)/larch (*Larix occidentalis*) and

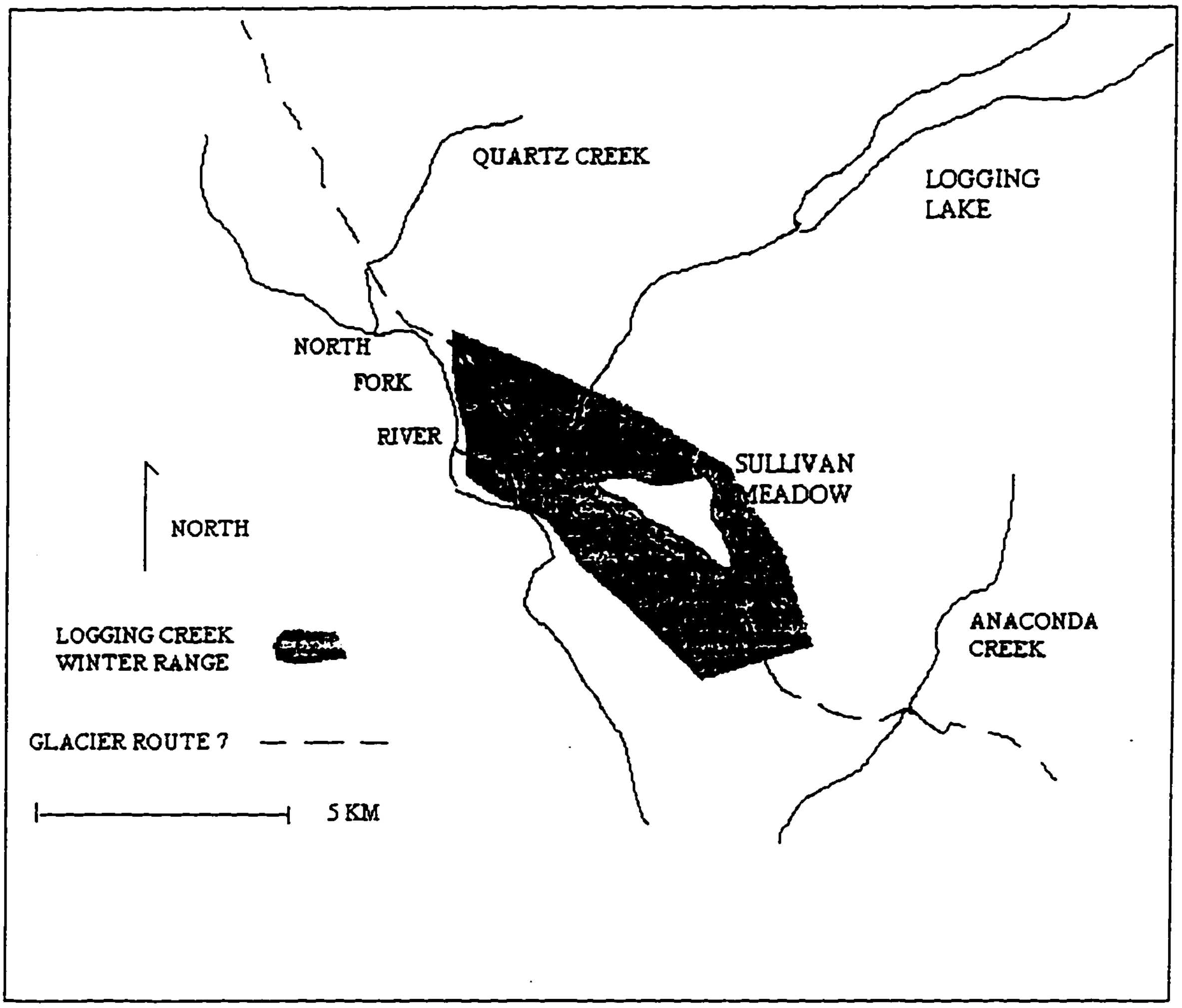

Figure 1. The Logging Creek winter range study area within Glacier National Park.

lodgepole pine (Pinus contorta) communities dominate the uplands. Much of the lodgepole was killed by beetles, and a low intensity fire burned the northern portion of the winter range in 1994. A large meadow (Sullivan) is a major feature of the winter range. Glacier Route 7 (unimproved dirt road) runs through the heart of the LWR but is not open during winter. Human use of LWR during winter is extremely low. We estimate that roughly 1000 deer, 50 elk, and 20 moose use LWR during winter.

The North Fork of the Flathead River drainage arguably has the highest density and diversity of large carnivores in North America. One wolf pack used the LWR and approximately 30-40 wolves in 3-4 packs occupied the greater study area (ca. 10 wolves/1000 km^2). The resident cougar population in the study area was estimated at 37-44 (ca. 10 cougars/1000 km^2, T. Ruth, Hornocker Wildl. Res. Inst., pers. commun). McLellan (1989) estimated the grizzly bear density to be 63 bears/1000 km^2 for southeastern B.C. and he estimated the black bear (Ursus americanus) density to be 3 times greater than that.

METHODS

Wolves were captured, sedated, and radio-tagged (Mech 1974, Ream et al. 1991). White-tailed deer were captured in traps (Clover 1956) in the LWR and females were fitted with radio collars. All radio-tagged wolves and a subsample of deer in the winter range were located simultaneously (within constraints of aerial telemetry), approximately once a week from the air. We attempted to obtain visuals of each animal we located. Structural class, cover type, and percent canopy coverage were recorded for each location (Table 1; chapter 3). Percent canopy cover was classified based on the examples in appendix B of Unsworth et al. (1991). Locations were plotted on aerial color photos and later transferred to 1:24,000 U.S. Geological Survey maps to determine Universal Transverse Mercator (UTM) coordinates. Starting in 1994, UTM coordinates were also obtained from a global positioning system (GPS) receiver onboard the airplane.

Deer and wolves were also located using ground telemetry (> 2 times/week) by skiing along Glacier Route 7 through the winter range (Fig. 1). Sites ("stations") along this route that consistently yielded reliable azimuths were numbered and their UTM coordinates were determined with a GPS receiver. Three or more bearings were taken on every radio-tagged deer from ground stations. Only deer whose signal was strong enough to reliably estimate an azimuth were triangulated.

To measure accuracy and precision of bearings, an independent observer placed radio collars at 4 locations in the area used by the radio-tagged deer. All project personnel (7) located these collars using the same technique used to locate deer. Mean bearing error (bias) and standard

Table 1. Canopy cover classes and size classes used by deer (based on ground locations) in the presence and absence of wolves in Glacier National Park, 1990-1995.

Variable	wolves present % of observations	wolves absent % of observations
Canopy		
low (15-39%)	45	54
medium (40-69%)	43[•]	31[•]
high (70-100%)	12	15
	n = 146	n = 249
Size Class		
seedling (<12.7 cm)[1]	6	10
pole (12.7-22.9 cm)	5	11
medium (23.0-53.3 cm)	39	42
large (> 53.3 cm)	44	34
low shrub (<76.2 cm)	6	4
	n = 158	n = 262

[•] P = 0.08

[1] diameter at breast height for trees; total height for shrub

deviation (precision) were calculated following White and Garrott (1990:82). This standard deviation was then used in the LOCATE II software (Pacer 1993) to plot locations of deer.

Triangulations of these deer were plotted using LOCATE II software. Confidence ellipses were generated for each location using the Tukey estimator (Lenth 1981). Only locations with confidence ellipses < 100 ha were used. Locations were used to generate home ranges for each deer with the adaptive kernel method in CALHOME (Worton 1989, Kie et al. 1996).

Wolves were classified as absent if their radio signals could not be heard while locating deer, and no fresh sign of wolves (tracks, kills, scats, or howling) was found in the winter range. Wolves were classified as present in the winter range if they could be successfully located in the winter range or if sign indicated they were present within the preceding 24 hours. We estimated the minimum number of consecutive days wolves were present in the LWR and the maximum number of days wolves were absent based on the days we monitored the LWR. These are minimums and maximums because we didn't monitor the LWR every day of the winter.

We used multiresponse permutation procedures (MRPP; Mielke et al. 1976) to compare distributions of locations of radio-tagged deer when wolves were present to locations when wolves were absent. Multiresponse permutation procedures compare the intragroup average distances with the average distances that would have resulted from all the other possible combinations of the data under the null hypothesis of no difference in distributions. The MRPP was does not require normality or equal variances between groups (Zimmerman et al. 1985). The P values (calculated using program BLOSSOM [Slauson et al. 1994]) indicate the probability that the distribution of deer locations in the presence and absence of wolves were the same. We could never be totally certain that wolves were not present; therefore, we used the excess option in BLOSSOM. In this option, the absent group may contain locations when wolves could have actually been present. This risk of misclassification is treated as background noise by BLOSSOM. The Spearman rank correlation test was used to compared sizes of deer home ranges in the presence vs absence of wolves.

Universal Transverse Mercator coordinates of deer locations were entered into a geographic information system (PAMAP GIS). Spatial and vegetative attributes were estimated (30 m minimum mapping unit) for each site from GIS map layers of the study area created by Singleton (1995) and Redmond (1996). Cover type, vegetation size class, canopy coverage, and modified normalized difference vegetation index (NDVI; a measure of absorption variation in middle infrared wavelengths which are know to be associated with canopy closure; Butera 1986, Redmond 1996) were obtained. We created canopy cover, cover type, and size class polygons (patches) from which we could estimate area, perimeter, and distance to edge of the polygon.

Habitat and spatial attributes at locations when wolves were considered present were compared to those when wolves were considered absent to test whether wolf presence affected habitat use by deer. These comparisons tested the null hypotheses that habitat and spatial attributes used by deer did not differ with the presence or absence of wolves. Mann-Whitney $\underline{U}$ statistics were used to compare differences in continuous variables. We used Pearson Chi-square analysis for categorical variables to test the null hypotheses of independence among categories. When > than 20% of cells had expected values < 5, we combined adjacent (similar) categories. Adjusted standardized residuals ([observed - expected/expected$^{0.5}$]/standard error) were used to identify significant cells (Habermann 1973). Probability values were adjusted by multiplying by the number of cell pairs in the cross-tabulation (Bonferroni adjustment-e.g. overall $\underline{P}$ = 0.001 and cell pairs = 5 , 0.001*5 = 0.005; Rice 1989).

We used habitat and spatial variables and stepwise logistic regression (Norusis 1993, Trexler and Travis 1993, chapter 3) to predict the probability of successfully classifying sites used by deer in the presence and absence of wolves (dependent variable). Independent variables examined were the same as in the univariate tests. The least explanatory of highly intercorrelated variables was not used during model building to reduce the likelihood of inaccurate results resulting from multi-collinearity (Trexler and Travis 1993). Variables were entered into the model at the 0.10 significance level and removed at the 0.11 level using the likelihood-ratio test (Norusis 1993). The Wald statistic was used to test whether the coefficient of individual classes of categorical variables was different from zero. Final models were assessed for reliability using goodness-of-fit maximum likelihood estimates, accuracy of classification tables, and significance tests of coefficients (Norusis 1993, Trexler and Travis 1993).

Giving-Up-Density

We tested the hypothesis that there was no difference in predation risk in habitats with high versus low stalking cover by comparing feeding rates of deer in both. Deer in the Logging Creek winter range were presented pre-measured amounts of food (110 g of dried, compressed alfalfa pellets) in wooden trays (46 X 30 X 12 cm) mixed with 2,070 cm^3 of nonedible substrate (pieces of white plastic tubing). The mixture ensured that feeding efficiency declined with time spent exploiting a tray as less food and more substrate was available. The experiment was conducted for 13 days in

February 1996. Trays were left in the field 24 hours after which the remaining food was removed and weighed to obtain the giving-up-density (original weight minus final weight). Fresh snow was spread around the trays daily so we could detect deer presence and ensure that only deer were eating from the trays.

Replicates of 3 stations with 2 trays each were placed in habitat types with low stalking cover (mean stalking cover total = 5) and 3 stations with 2 trays each (10 - 30 m apart) were placed in habitat types with high stalking cover (mean stalking cover total = 19). Percent stalking cover was determined by visually estimating the percent of a deer obscured at 30 m in the 4 cardinal directions from one box at each station (chapter 3). Stalking cover was divided into 5 categories: 1) 0-10%, 2) 11-30%, 3) 31-50%, 4) 50-75%, and 5) 76-100%. The sum of the cover classes from the 4 directions was the stalking cover for the site. All sites were located along heavy (chapter 3) deer trails. Mean canopy cover was 63% at closed sites and 33% at open sites; mean snow depth was 9.5 cm at closed sites and 4.6 cm at open sites; edge of cover type was not visible at closed sites and was visible at open sites; upland spruce dominated closed sites and ponderosa pine (Pinus ponderosa) and burnt Douglas-fir dominated open sites; and deadfall height averaged 12.9 cm at closed sites and 20.2 cm at open sites. The sites presented deer with similar energetic foraging costs and missed opportunity costs. We attributed any GUD differences between sites to variation in predation cost related to safety of habitat (Kotler et al. 1994).

RESULTS

Mean elapsed time required to obtain each ground radio-tracking location was 28.4 minutes (SE = 0.6, n = 525). Mean bearing error (bias) based on locations of test collars was 1.6° and standard deviation (precision) was 16.1° (n = 74 bearings). Mean distance error based on 27 locations of test collars (excluding one outlier) was 266.2 m (SD = 194.7 m). Mean area of confidence ellipses was 35.4 ha (SE = 3.4, n = 606).

The South Camas pack (wolf pack using LWR) consisted of 7 wolves (4 radio-tagged) in spring 1991, 5 wolves (2 radio-tagged) in spring 1992, 14 wolves (3 radio-tagged) in winter 1993, 19 wolves (4 radio-tagged) in winter 1994, and 11 (2 radio-tagged) wolves in winter 1995. Wolves were present in the Logging winter range 28 (40%) of 70 days they were monitored from 1993-95. Wolves remained in the winter range for an average of 1.6 days (SE = 0.16, range = 1 - 4 days). The mean number of days between visits to the winter range was 5.4 days (SE = 0.7, range = 1 - 16 days).

The distribution of radio locations of 4 deer out of 10 were significantly different when wolves were in LWR than when they were away (P < 0.05). The location of another deer was marginally different (P = 0.07) in the presence of wolves if wolves were only considered present when they had been in the LWR for 2 or more days and were considered absent only if they had been away 2 or more days.

The distribution was marginally different in the presence versus the absence of wolves ($\underline{P} = 0.08$) when locations of all 10 deer were grouped for all years and the 2 or more day restrictions were used. Deer home range size was not correlated with wolf presence (75% adaptive kernal home ranges; Spearman correlation coefficient = 0.0260, $\underline{P} = 0.913$).

The median canopy cover used by deer was greater when wolves were present (med= 60%, SD = 25.8, $\underline{n} = 49$) than when wolves were absent based on aerial (med = 45%, SD = 19.7, $\underline{n} = 61$; Mann-Whitney $\underline{U}$ (MWU) $\underline{Z} = -2.138$, $\underline{P} = 0.033$) and ground locations ($\chi^2 = 4.99$, 2 df, $\underline{P} = 0.082$; Table 1).

There was no difference in structure class used when wolves were present versus absent based on aerial locations ($\chi^2 = 2.10$, 1 df, $\underline{P} = 0.147$; Table 2). However, deer used higher size class categories in the presence versus the absence of wolves based on ground locations ($\chi^2 = 9.55$, 4 df, $\underline{P} = 0.049$; Table 1).

There was no difference in cover types used by deer when wolves were present or absent based on aerial ($\chi^2 = 1.6$, 4 df, $\underline{P} = 0.81$; Table 2) and ground locations ($\chi^2 = 3.78$, 5 df, $\underline{P} = 0.582$; Table 3).

Based on ground locations, deer used areas closer to

Table 2. Cover and structural classes used by deer (based on aerial locations) in the presence and absence of wolves in Glacier National Park, 1993-1995.

Class	wolves present % of observations	wolves absent % of observations
Cover Type		
Open/shrub	8	5
Burnt timber	24	19
Larch/Ponderosa	18	16
Lowland Conifer	6	3
Lodgepole	24	31
Upland spruce	6	8
Douglas-Fir	16	18
	_n_ = 51	_n_ = 62
Structural Class		
Non-vegetated	0	0
Herbaceous	5	7
Shrub/seedling	0	0
Sapling	0	0
Pole/sapling	0	0
Young trees	0	7
Mature trees	95	86
	_n_ = 100	_n_ = 100

Table 3. Cover classes used by deer (based on ground locations) in the presence and absence of wolves in Glacier National Park, 1990 -1995.

Class	wolves present % of observations	wolves absent % of observations
Grassland	3	3
Douglas Fir	16	9
Juniper	3	4
Larch	7	6
Mixed mesic	60	66
Mixed xeric	12	12
	n = 148	n = 249

the edge of canopy cover polygons (MWU $\underline{Z} = -1.86$, $\underline{P} = 0.063$; Table 4) and cover type polygons (MWU $\underline{Z} = -2.37$, $\underline{P} = 0.018$) when wolves were present than when they were absent. Size class perimeter and area used by deer was lower in the presence versus the absence of wolves (MWU $\underline{Z} = -1.79$, $\underline{P} = 0.073$, MWU $\underline{Z} = -1.79$, $\underline{P} = 0.074$, respectively; Table 4). The median NDVI used by deer was greater (MWU $\underline{Z} = -1.65$, $\underline{P} = 0.10$; Table 4) in the presence versus the absence of wolves.

The simplest multivariable logistic model that predicted ($\chi^2 = 19.05$, 5 df, $\underline{P} = 0.0019$) the probability that a specific location would be used by deer in the presence of wolves ($\underline{p}$) used size class, NDVI, and area of size class (Table 5):

$$1 - \underline{p} = \frac{1}{1 + \underline{e}^{-Z}}$$

where $\underline{Z}$ = constant + $\underline{B}$ (variable 1) + $\underline{B}$ (variable 2) + $\underline{B}$ (variable n). The probability that the site is used by deer when wolves were present increases if the coefficient in Table 5 is positive and decreases if it is negative. Greater levels of NDVI, larger size classes, and smaller areas of size class patches increased the probability that a site was used in the presence of wolves. The model's overall prediction success decreased from an initial value

Table 4. Use of habitat and landscape features by white-tailed deer when wolves were present (*n* = 158) versus when wolves were absent (*n* = 262) in Glacier National Park, Montana from 1990-1995.

	wolves present		wolves absent	
Variable	$\bar{x}$	SD	$\bar{x}$	SD
Distance[1] to canopy polygon edge	98.7	131.7	78.0*	125.6
NDVI[2]	359.0	160.4	330.4*	152.1
size class polygon area[3]	2985	2484	3177*	2526
size class polygon perimeter	237251	197675	258927*	206495
Distance to size class polygon edge	73.1	65.5	80.4	69.5
cover type polygon area	9138	8564	10465	8377
Distance to cover type polygon edge	90.1	93.0	113.3**	105.1

** $P < 0.05$

* $P < 0.10$

[1] meters

[2] normalized difference vegetation index; Nemani et al. (1993)

[3] square meters

Table 5. Logistic regression results from wolf presence versus wolf absence comparison in Glacier National Park, Montana, 1990-95.

Variable	Coefficient	SE	Log LR[1]	Wald[2]
NDVI	0.003	0.001	0.025	0.027
SC area[3]	-0.000	0.000	0.025	0.025
Size Class			0.004	0.006
Seedling	-0.208	0.355		0.558
Pole	-0.979	0.396		0.007
Medium	0.692	0.245		0.005
Large	0.495	0.269		0.066
Constant	1.441	0.457		0.002

[1] likelihood ratio P value

[2] P value associated with Wald statistic

[3] area of size class polygon

of 63.0% to a final value of 61.8%.

Giving-Up-Density (GUD)

Deer first ate out of a GUD tray on day 6 of the experiment. This tray was in the sparse stalking cover class. They ate most to all of the pellets out of this tray on this day and the remaining 7 days of the experiment. On day 8 they ate from the other tray at this site and continued to do so for the remainder of the experiment. On day 12 deer ate from 2 additional trays (paired) in the sparse stalking cover class and did again on day 13. On the final day of the experiment (day 13), deer ate from the 2 remaining trays in the sparse stalking cover class. Food in the dense stalking cover class was never consumed. Wolves were present in the LWR on days 10-12 of the experiment.

DISCUSSION

Strategies used by white-tailed deer to avoid wolves during winter revolve around concentrating in yards (Nelson and Mech 1981, Messier and Barrette 1985). Similar to herding, this strategy serves to reduce risks to individuals through increased detection of predators (Kenward 1978), greater confusion of predators in pursuit (Jarman 1974), and a sharing of risks (Hamilton, 1971, Nelson and Mech 1981). Individual encounter and detection rates by predators may be reduced due to a dilution effect. Deer may also reduce encounter and detection rates by spacing away from predators

(Bergerud and Page 1987) and moving to areas with greater hiding cover when predators are present (Geist 1981). Deer near other deer being chased by hounds moved away from the disturbance, sometimes into dense cover and swamps (Sweeney et al. 1971). Dasmann and Taber (1956:155) concluded that within their home range, black-tailed deer usually had a preferred area for escape.

We found that deer avoidance of predation by wolves occurred at 2 levels. At the first level, deer shifted away from centers of wolf activity when wolves moved into the LWR to reduce chances of encounters and detection and concurrently moved into denser cover to further reduce detection. When wolves moved into the LWR, they spent most of their time in Sullivan Meadow (K. Kunkel, unpubl. data). All the deer that shifted location in the presence of wolves were on the edge or nearest to Sullivan Meadow and shifted away from the meadow. Only one deer in or on the edge of the meadow did not shift in response to wolves. These shifts away from the meadow also corresponded to movements into higher levels of canopy coverage. Deer that did not shift ranges were on the west side of Glacier Route 7 (Fig. 1). Deer apparently respond to the presence of wolves (and humans, K. Kunkel, unpubl. data) by shifting away from wolves and moving into thicker cover, but because these are correlated in LWR, it is difficult to determine which is more important. The strategy outlined above reduces encounter and detection of individual deer by predators.

The second level at which deer reduce their predation risk is by reducing capture rates of predators through reliance on early detection of predators and quick escape (Mech 1970, Mech 1984, chapter 3). It follows that habitats offering enhanced detection of predators or alternately reduced stalking cover for predators offer greater security from predation (chapter 3). Our results support that idea. Based on giving-up-densities, deer regarded more open habitats as safer. LaGory (1987) reported that flight distance of deer is greater in more closed habitat types suggesting that deer are more wary there. These areas increase the risk of capture by wolves and cougars (chapter 3). We believe that overall, deer are more secure in more open habitats, unless these happen to be near centers of wolf activity.

We urge some caution in the interpretation of our GUD results. Deer use of our feeding trays increased over the course of the experiment indicating that it may have taken some time for deer to discover these sites or feel comfortable eating from the trays. Although none of the food in dense cover was consumed, density and activity of deer (based on tracks and density of deer trails) was similar to density and activity of deer near the sites in sparse cover. We recommend conducting this experiment to make further tests of relative security values of differing habitats but suggest prebaiting first to reduce the possible wariness of deer to feeding trays and respond immediately at the initiation of the experiment.

In addition to moving away from wolves and into denser hiding cover, shifts in deer distribution may have also been correlated with density of deer. In the presence of predators, deer may move to areas with higher deer densities to accrue increased benefits of the dilution effect and to increase predator confusion. Messier and Barrette (1985) believed the mechanism most influential in reducing deer vulnerability to predation in deer yards was the greater number of runways in higher deer density areas. These runways (trails) increase ease of escape. Our breakdown of classes of deer density within LWR was too gross to test this. Increases in group size in response to the presence of predators (a phenomenon analogous to the one described above for deer) have been reported for many species including ungulates (Heard 1992, Jedrzejewski et al. 1992).

Shifts in distribution by some deer and not others may have been a result of their location with respect to Sullivan Meadow (as discussed above) but it also may be a result of other factors. Vulnerability to predation may decline with age and experience with predators. Young animals may be predator-naive and have to learn how to reduce their exposure to predators (Curio 1993) and, as a result, may experience higher predator-caused mortality rates (Dickman 1992, Rohner and Krebs 1996). Deer in our study ranged from 2.5 - 7.5 years old. There was no difference in mean ages of shifting versus nonshifting deer. Future studies should examine a larger sample of deer including more younger animals to fully access this effect. Nutritional condition of animals also affects exposure levels to predation. Animals in poor condition may not respond to increased risk of predation if it forces them to move away from foraging areas (Sinclair and Arcese 1995). Further, animals in poorer condition may tolerate a closer distance to an approaching predator before escaping (Rohner and Krebs 1996). While we have no data on the relative condition of the animals in our study, survival of nonshifting deer was lower (3 of 5 were killed by predators) than survival of shifting deer (1 of 5 was killed by predators). Two of the nonshifting deer were killed in the LWR during winter, one by wolves, one by a cougar. Further, shifting deer may have had direct contact with wolves thereby knowing they were present while nonshifting deer might not have had this contact and may have been unaware of the presence of wolves. Nonshifting deer may also have had escape habitat available nearby and may not have needed to shift to attain it. Additionally, some deer may not perceive little or no risk in the absence of a predator and may always behave as if risk is high. As a result, we might expect little change in behavior in response to presence of predators (Lima and Dill 1990). Finally, experience with other predators may shape the behavioral response. If a particular deer has encountered cougars more than wolves, it may behave in a way most likely to reduce its risk of capture by cougars.

Habitats may offer differing predator avoidance and predator escape values and prey must often make tradeoffs. Based upon mathematical modelling of the relative values of these 2 habitat values, Lima (1992) believed that prey should prefer the habitat in which the escape tactic is most effective even at the risk of greater encounter with predators. In the case of deer on winter ranges, habitats with low levels of stalking cover should then be preferred in all situations. We did not find this to be the case, but rather deer were very plastic in their response to predators. This should not be too surprising; research on Savannah sparrows (*Passerculus sanwichensis*) has indicated that these birds "track predation risk and make appropriate adjustments on a very fine (minutes to hours) time scale." (Watts 1991:1518).

Investigation of wolf scats by deer (K. Kunkel, pers. obs.) may be one way deer learn of the presence or absence of wolves. Ozoga and Verme (1986) indicated that females may move their newborn fawns significant distances from areas where coyote (*Canis latrans*) urine is found. Muller-Schwarze (1972) showed that black-tailed deer (*O. hemionus*) would not feed in the presence of predator feces. Odors of predators have been found to illicit shifts in habitat use in other prey species also (Jedrzejewski and Jedrzejewski 1990, Dickman 1992).

Resource Depression

Charnov et al. (1976) were the first to recognize that the presence of a predator may induce changes in prey behavior which would lower their vulnerability to the predator. They termed this phenomenon "resource depression." White-tailed deer in our study area responded to the presence of wolves by shifting distributions and habitat use. They may also have exhibited greater alertness and wariness in the presence of wolves (Kunkel unpubl. data) similar to the response of elk to wolves in Alberta (Huggard 1993). Whether these shifts in habitat use and behavior resulted in reduced vulnerability to predation is not known. We didn't have enough continuous wolf tracking data from the LWR to determine if wolf kill rates declined with the number of days wolves were present in the yard. However, the mere fact that wolves did not hunt in the LWR all winter long may indicate that reduced vulnerability of deer, and the resulting low kill rates, may have forced wolves to move to other winter ranges to increase their rate of success. Wolves were present in the LWR for 2 days on average and were away for 5 days. When they were not hunting in the

LWR, they were hunting at the other 2 winter ranges in their territory or they were hunting scattered groups of elk, moose and deer. Carbyn (1983) also reported that wolves did not remain in individual areas of high prey density, and Fritts and Mech (1981) reported that kills were distributed more uniformly than prey. Both of these patterns indicate that kills cannot be made repeatedly in one herd. For this reason, Huggard (1993) chose herds rather than individuals as the unit of encounter by wolves.

An alternate reason that wolves may have left the LWR was to patrol and scent mark in other portions of their territory (W. C. Gasaway, Wildlife Services, pers. commun.). But even this may result from resource depression. Charnov et al. (1976) predicted that predators of depressible prey should be territorial and the size of their territory should be related to the disturbance-recovery-disturbance cycle. Jedrzejewski and Jedrzejewski (1990) indicated that weasels (Mustela nivalis) depressed their prey for days. To overcome this, weasels minimized the time spent in any one area and prolonged their return to it, producing a rotational use of their home range. Similar phenomenon have been reported for marten (Martes martes), lynx (Lynx lynx), bobcats (Lynx rufus), and owls (Strix aluco and Aegolius funereus; cited in Jedrzejewski and Jedrzejewski 1990). Additional research directed at examining kill rates in relation to time spent in a patch is needed to further clarify this issue.

The time between initial depression and when a predator can profitably return to a patch is termed "return time" (Charnov et al. 1976). If wolves are indeed behaving as predicted by a resource depression model, return time in LWR averaged 5 days. Weaver (1994) reported that wolves in Alberta revisited the same patch of elk every 14 days and the same patch of sheep (_Ovis canadensis_) every 22 days. He believed wolves only got 1 or 2 opportunities to kill elk in a herd before the animals became too alert and coalesced. Resource depression in elk results primarily from herding behavior whereas in white-tailed deer, resource depression may result from both grouping behavior and shifts in habitat use. As a result, return times for deer may be longer than return times for elk. Certainly other factors such as wolf territory size and prey density and dispersion also affect this. More work is needed in this area (similar to that initiated by Erwin 1989) because this has important implications for vulnerability of different prey species and thus selection by predators.

Wolves recolonized the North Fork area in the early 1980s after nearly a 50-year absence. In response to the absence of wolves, deer may have altered their behavior and habitat use and may now again be altering their behavior and habitat use in response to the return of wolves. Breitenmoser and Haller (1993) reported that the return of lynx to Switzerland after a 150-year absence may have changed the anti-predator behavior of roe deer (Capreolus capreolus). They speculated that alert behavior in deer changed and that readaption occurred within 10 years of recolonization. This might be considered as resource depression on a large scale. Similar phenomenon have been described for alteration in group size of musk-ox (Ovibos moschatus) in response to wolf presence (Heard 1992). It is unclear whether the absence and subsequent return of wolves in our study area has had any measurable effect on prey behavior, but giving the highly plastic response of deer, we expect it did.

Predator Facilitation

White-tailed deer on winter ranges in our study area must balance their exposure and risk of predation to the 2 apex predators in North America, wolves and cougars. While hunting success of both these predators in our study area is highest in denser stalking cover (chapter 3), wolves are certainly also efficient predators in open habitats. Several factors determine areas selected by deer within winter ranges including snow depths, browse availability, and security from predation. Higher levels of canopy coverage reduce snow depths, but these areas have lower browse production (Potvin 1978) and generally greater levels of stalking cover. Deer in the LWR selected denser canopy in the presence of wolves. This likely placed deer at greater risk for predation by cougars (chapter 3).

Very little research has been directed at examining response of prey to multiple predators. In an experiment using captive gerbils (Gerbillus allenbyi and G. pyramidum), Kotler et al. (1992) reported that in response to the presence of greater sand vipers (Cerastes cerastes), gerbils increased their exposure to eagle owls (Bubo bubo). Charnov et al. (1976) termed this predator facilitation. Introduction of weasels (Mustela nivalis) into a captive environment containing voles (Microtus agrestis) caused voles to shift from cover to more open areas and potentially increased their exposure to kestrels (Falco tinnunculus). However, when kestrels were also present voles remained in cover (Korpimaki et al. 1996). This implied voles viewed kestrels as a greater threat. Apparently, deer in our study area viewed the arrival of wolves as a greater threat than the constant presence of cougars on their winter range, even though wolf and cougar-caused mortality rates on deer are very similar in our study area (chapter 2). Without such shifts, wolf-caused mortality rates may have been higher.

Balancing avoidance of 2 predators probably makes life more costly. This balancing act probably increases energy demands on deer and also reduces foraging opportunities and this results in deer in poorer condition (Batcheler 1968, Hik 1995) and ultimately makes them even more susceptible to predation.

Telemetry Error

Results of habitat use by deer based on locations triangulated on the ground were similar to those based on locations from the air, suggesting that precision from the ground was adequate for the level of analysis we performed. Only our findings of a difference in use of structural size classes differed between aerial and ground telemetry. Given that the mean distance error from ground telemetry was relatively large compared to the mean distance of locations of deer from the edges of patches, this result should be interpreted with caution. We do believe that little error resulted due to the time it took to complete a ground location ($\bar{x}$ = 28 minutes) because we determined the mean straight-line distance moved by 4 deer for this interval (based on snow-tracking) was only 40 m.

Logistic Model

The correct classification of sites in the logistic model we developed was lower than the initial classification. This probably results from model misspecification (i.e. possibly not including prey density or other important parameters in the model). We believe this model is theoretically important, but the application value remains to be tested. We advocate applying the recommended prescriptions (see below) as experiments conducted as integral parts of management programs (MacNab 1983, Walters and Holling 1990, Clark and Nudds 1991) that include measuring wolf and cougar predation rates and/or deer survival rates.

MANAGEMENT IMPLICATIONS

Where multiple predators exist or where behavioral or habitat changes occur in prey in response to predators, depression due to these factors may be more important than exploitation depression (Charnov et al. 1976). As a result, we believe that one strategy that could be potentially used by managers to reduce predation rates on deer is to concentrate deer into fewer winter ranges. By concentrating deer into fewer, larger yards, anti-predator benefits of yarding are maximized as is resource depression. In this circumstance, deer will maintain behavioral and habitat shifts that minimize predation. As a result, it is possible wolf kill rates will be reduced. However, wolves may respond to this by "hunting harder" to maintain their kill rate or they may switch to alternate prey (Potvin et al. 1988). It is possible, however, that the few large yard strategy may increase stress levels in deer due to the increased amount of time wolves remain in a yard. This increased presence of wolves may reduce foraging rates, thereby placing deer in poorer condition. More research is needed on this.

Our results also point to the critical importance of providing the optimum mix of security habitat that reduces exposure to multiple predators but still provides foraging opportunities. We have outlined specific recommendations for this elsewhere (chapter 3).

Predator/prey relationships are exceedingly complex. The traditional examination of only outright mortality caused by predators and the influence of animal condition parameters only on this severely limits our knowledge of predator/prey systems. Future research must be directed at the effects of predators on habitat use and behavior of prey and must examine how spatial and habitat features influence vulnerability of prey. This avenue of research offers great potential for innovative approaches to predator and prey management that goes beyond traditional predator control remedies. This is exceedingly important as habitats are increasingly modified by humans and as human values toward predators change.

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