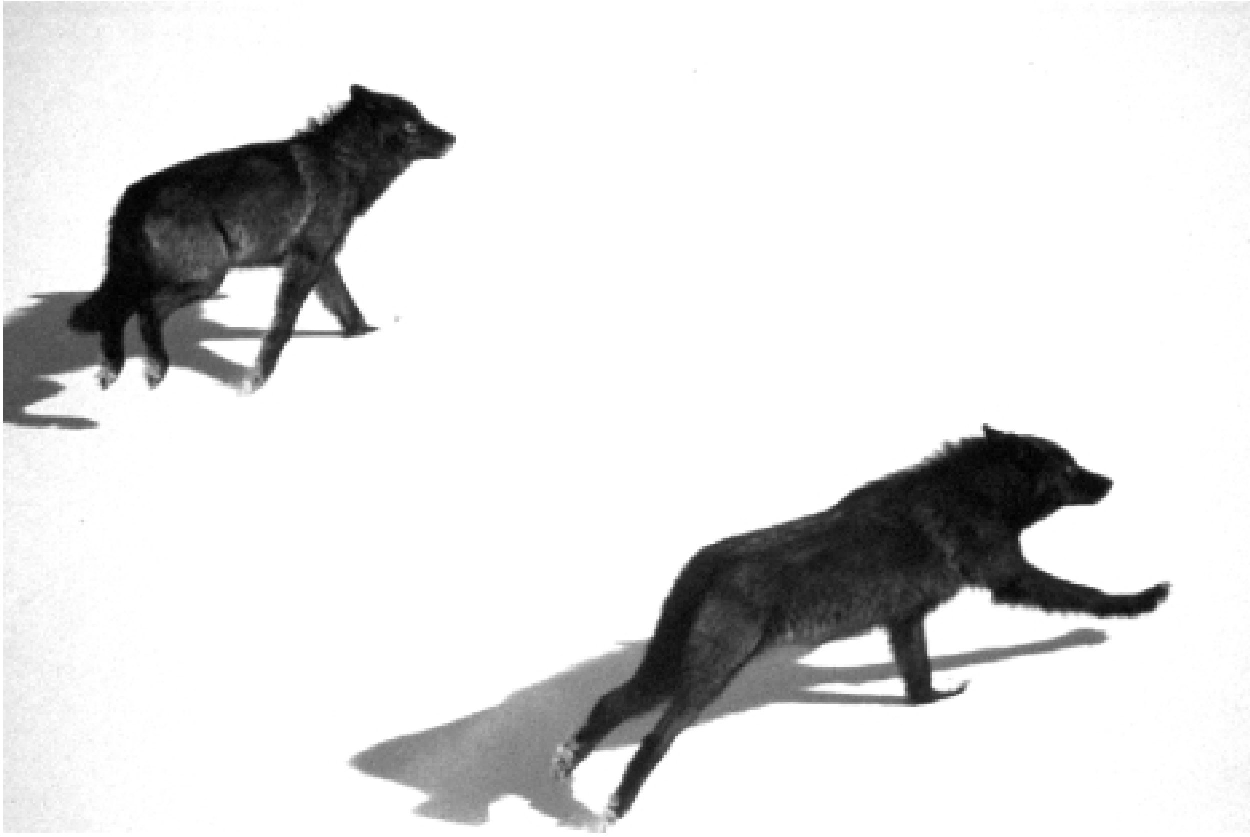
WOLF AND ELK PREDATOR-PREY DYNAMICS IN BANFF NATIONAL PARK



by
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Central Rockies Wolf Project

WOLF AND ELK PREDATOR-PREY DYNAMICS
IN
BANFF NATIONAL PARK

By
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Bsc. University of Guelph, 1995

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Wolf and Elk Population Dynamics in Banff National Park (130 pp).

Director: Daniel H. Pletscher

Abstract:

Wolves (*Canis lupus*) recolonized the Canadian Rockies in the mid 1980's after a thirty year absence. I studied wolf and elk (*Cervus elaphus*) population dynamics during the winters of 1986 to 2000 in Banff National Park (BNP), Alberta. Elk are the primary prey of wolves in BNP, differing from other major prey species by living in herds. I studied how elk herding affected predation by wolves. Wolves encountered larger elk herds more than expected based on availability, and wolf attack success on larger elk herds was higher than expected based on encounters. Wolf selection for larger elk herds, combined with increasing herd size with elk density, may affect the functional response of wolves preying on elk. Individual elk still benefited from living in herds, and predation by wolves links individual behavior of elk to population dynamics.

Quantitative assessment of the effects of wolves on elk populations requires estimating wolf kill-rates. I developed a statistical estimator for winter kill-rates for five wolf packs from 1986 to 2000. The mean total kill-rate (not equal to consumption rates) was 9.5 kg of prey/day/wolf, or 0.33 kills/day/pack (k/d/p). Mean total kill-rates were composed of 0.23 elk/d/p, 0.04 mule deer/d/p, 0.03 white-tailed deer/d/p, 0.02 bighorn sheep/d/p, and 0.01 moose/d/p. Kill-rate estimates were variable despite intensive sampling. Elk kill-rates explained 93% of the variation in total kill-rates, suggesting low potential for prey switching within the relatively high elk densities we observed.

Lastly, I studied factors affecting elk population growth rates in the Bow Valley of BNP over a 15-year period using a pseudo-experimental approach in three zones that differed in relative wolf use and contained separate sub-populations of elk. High human use in the central zone of the Bow Valley reduced relative wolf density. In this zone, elk population growth rates and population size appeared regulated by elk density. By contrast, with predation by wolves, a combination of snow depth and wolf predation limited elk population growth rates. My research characterizes differences in ungulate population dynamics with and without predators, and suggests predation by wolves can limit elk in multiple prey systems.

Preface

In 1987, Parks Canada initiated a study of wolves recolonizing the Bow Valley of Banff National Park (BNP). The first wolf pack since the 1950's denned in the Bow Valley of BNP in 1986, and the Banff Warden Service radio-collared a wolf from this pack in the winter of 1986/87. In 1989, Parks Canada contracted Dr. Paul Paquet to lead a regional research program investigating the ecology of recolonizing wolves, and Dr. Paquet initiated the Central Rockies Wolf Project. University of British Columbia Master of Science student David J. Huggard completed his graduate research in cooperation with this contract. This contract ended in June 1993, and was continued by the Banff Warden Service and Dr. Paul Paquet until 1994/95, when University of Guelph Doctoral candidate Carolyn Callaghan took over direction of the research in Banff National Park. In 1997 I began my contract with Parks Canada to study wolf and elk population dynamics in response to recommendations in the government task force, the Banff Bow Valley Study, and the new BNP management plan. Other cooperating agencies during this period included Alberta Environment Protection, Kananaksis Country, Kootenay and Yoho National Parks, Mount Assiniboine Provincial Park, and British Columbia Ministry of Environment, Lands, and Parks. This 15-year cooperative research project provided me with a unique opportunity to research wolf and elk population dynamics over a 15-year period in Banff National Park.

The following thesis contains three manuscripts (chapters 2, 3, &4) stemming from research completed during my graduate degree, and include data collected throughout the extended length of this study. Chapter 2 (on elk herding) was a novel area of research conducted during my intensive study period from 1997 to 2000. In chapter 3, I used wolf predation and monitoring data collected since the first wolf was radio-collared in 1987, including data collected under contract by Dr. Paul Paquet and as part of Carolyn Callaghan's Ph.D. Therefore they will be co-authors on the final manuscript when submitted for publication. Chapter 4 uses these data on wolf predation and a 15-year time series of elk population counts collected by the Banff Warden Service as part of annual monitoring. Because of Dr. Paul Paquet's involvement with data collection and study design over the entire period of the research, he will be co-author on this final manuscript as well. Dr. Daniel H. Pletscher will be a co-author on all three chapters due to his very important role during all of my research. My co-authors acknowledge my senior role in conducting this research as part of my Master in Science graduate degree, and I will be lead author on all manuscripts submitted for publication from this thesis. Due to the collaborative nature of this research, I have used 'we' instead of 'I' in the three chapters. I directed the field work for chapter 2, and 3 years of field work for chapters 3 and 4, did all of the data analysis and writing and take full responsibility for any errors contained in this thesis.

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A project of this length has benefited from the assistance of many people and organizations, and I have many to thank. I appreciate generous financial, logistical, and in-kind support from Parks Canada, the Central Rockies Wolf Project, Alberta Human Resources and Employment, Human Resources Development Canada, John/Paul & Associates, Canadian-Pacific Foundation, Friends of Banff National Park, Paquet Wildlife Fund, Peter W. Busch Family Foundation, World Wildlife Fund, and the Dr. Joseph Paquet Wildlife Fund at University of Montana. Patagonia, Marmot, and Garmin GPS provided field equipment. The Les Pengelly and George Bright Memorial Scholarships in the School of Forestry at the University of Montana provided support for me while I was in residence.

My research would have been impossible without the 15-year research foundation upon which it was built. I thank my colleagues with the Central Rockies Wolf Project (CRWP), especially Dr. Paul Paquet and Carolyn Callaghan. Paul deserves due credit for initiating the project in the late 1980's and for numerous helpful discussions on wolf ecology and conservation. Carolyn Callaghan deserves special thanks for providing a logistical umbrella, friendship, and advice. Other colleagues with the CRWP provided much in the way of stimulating discussions, friendship and support throughout my research, and I thank Shelley Alexander, Danah Duke, Scott Jevons, Timmothy Kaminski, Melanie Percy, Jesse Whittington, and Steve Wadlow.

I thank the research assistants (~50) who worked on the Banff wolf packs since 1987, many of whom I never had the privilege of working with during the last 5 years. I won't list them to avoid forgetting anyone, thanking them all instead for their dedication and contribution to wolf research and conservation. I would like to thank those whom I was personally involved with during my intensive research from 1997 to 2000, Stephen Anderson, Connie Atkinson, Matt Dragon, Sarah Goulet, Otso Huitu, Bridget McClarty, Danielle Robertson, Joachim Vos, and Jennifer Wasylyk. Special thanks to Timmothy Kaminski and Cedar Mueller for running the project during my time away at school. You all gave more than you were paid to this project, and although I'm sure it was due to the opportunity to work with such a fascinating animal as the wolf, I thank you anyway.

The Banff Warden Service provided assistance and data on elk populations, and I thank Tom Hurd and Cliff White for providing data, logistical assistance, support, and stimulating discussions on wolf-elk ecology and ecosystem management. They are also collaborators on the humans-wolves-elk-aspen-willow (HWEAW) ecology project, and I thank them for the opportunity to place my research in a greater context. Other Banff researchers that provided logistical support and assistance are Michael Gibeau, John McKenzie, Cliff Nietvelt, Saundi Stevens, John Paczchowski, and Martin Urquhart. John McKenzie and the elk research crew were invaluable for my research on elk herding. Thanks to the BNP warden service who provided assistance in innumerable ways throughout the research, especially wildlife wardens A.L. Horton, Dave Norcross and Tom Davidson.

Veterinary assistance and advice with wolf immobilization was provided by Dr.'s Todd Shury and Mark Johnson. Skilled and safe fixed-wing aircraft support was provided by Michael Dupuis of Wildlife Observation Service, Calgary. Rotary-wing aircraft support was provided throughout the study by a number of pilots from Alpine Helicopters of Canmore, and I thank them all for their safe flying, especially Alpine manager and pilot Lance Cooper whose excellence and sensitivity to animal care made aerial wolf capture safe and relatively easy. Special thanks to John Thornton of Banff Mount Norquay Ski Resort, who let me use their detailed records on snow depth for my analyses.

During my time at the University of Montana, my academic committee, Dr.'s Kerry Foresman, L. Scott Mills, and Paul Paquet, kept my research on the straight and narrow. Their job was relatively easy compared to my main advisor, Dr. Daniel H. Pletscher. By way of comparison, if the rest of my committee made sure I was on the straight and narrow, Dan, through countless and thankless excruciating hours, made sure I was even sea-worthy to start with. None of this would have been possible without his quick-thinking, flexibility, dedication to his students, and patience as I developed my skills during this thesis. Thank you Dan. I'd also like to thank Dr. Mark Lindberg for frequent discussions on data analyses, and his skill at opening up the black box of statistical analyses during coursework. Special thanks to the real head of the Wildlife Biology program, administrative guru Jeanne Franz, whose patience and assistance with an easily confused and often late foreign student kept me enrolled, on time, and in touch with my degree from a distance. Finally, friendship with fellow graduate students such as Michael Schwartz and John Citta at the UofM, and Peter Biro and Marco Musiani (University of Calgary), enriched my academic experiences.

My deepest thanks to my supportive family, especially my mum (British spelling), Eileen Bennett, whose unending support and advice landed me in the privileged position of conducting research on wolves in Banff. I also thank Bridget McClarty, who as my partner through the last part of my research was an unparalleled research assistant who put up with a demanding and distracted boss. Bridget's companionship through all of my analysis and writing are in a large part responsible for the retention of my sanity. Thank you Bridget. I would also like to thank my canine companion, Keta, who patiently pointed out the canine world to me and was the most faithful research assistant, collecting snow tracking data with a zeal for wolf scent unseen in other assistants. Keta's patience and enthusiasm for the world of the wolf allowed me to gain an understanding of wolves otherwise inaccessible to the human mind.

Finally I wish to express my deepest thanks to the wolves of Banff. The five years I spent tracking these wolves through the congested Bow Valley to the wilds of the front range backcountry of Banff have shown me there is still much that is wild in this world and much that is truly incredible to see. They have shown me a Banff unlike few other humans have ever seen, and I feel truly privileged to have had the opportunity to spend some time knowing what it is like to be a wolf in one of the most beautiful and threatened landscapes I know. My deepest hope is that this research contributes in some small way to this world retaining some of that wonder.

By the 1970s, when I was soaring and turning and circling over the dry bones of elephants on the barren plain at Tsavo, a curious situation had arisen, in which the accepted theories were failing to provide a successful basis for the management of living resources. It seemed to me that it is one thing to play games in a laboratory and pretend that nature is like an artificial container of fruit flies, but quite another to fool ourselves that such a game should be played out with the remaining treasures of wildlife and wild habitats in the realities of our complex and discordant world.

Daniel Botkin, Discordant Harmonies, 1990

Chapter 1. Introduction

As Botkin (1990) suggested in his example of the ecological disaster of elephant management in Tsavo National Park, management of living resources requires a firm ecological and theoretical basis, or it is doomed to repeat the failures of the past. Through dispersal (Boyd and Pletscher 1999) and active reintroduction (Fritts et al. 1997), gray wolves (*Canis lupus*) are poised to reclaim much of their former range through western North America in the lower forty-eight states. Central questions regarding recolonizing wolf populations revolve around the ecological impact of wolves on ecosystems and the ungulate populations in them. Debate over the impact of predation by wolves on northern ungulates have occupied managers and biologists for decades, and empirical and theoretical research suggests wolf predation may limit or even regulate ungulate populations in single prey systems (e.g., Gasaway et al. 1992, Dale et al. 1994, McLaren and Peterson 1994, Messier 1994, Van Ballenberghe and Ballard 1994, Boertje et al. 1996, Ballard et al. 1997, Jedrzejewska et al. 1997, Orians et al. 1997, Jedrzejewski et al. 2000).

Despite this knowledge, predicting the ecological impact of wolves in restored ecosystems is currently difficult to answer. Many of the areas where wolves are recovering are multiple prey systems where the dominant ungulate is elk (*Cervus elaphus*), with alternate prey species which could include mule deer (*Odocoileus* *hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), pronghorn (*Antilocapra americana*), and even bison (*Bison bison*). Researchers have only recently begun to study wolf-prey dynamics in multiple prey systems, and wolf-elk research does not benefit from long-term quantitative studies. Managers and researchers in wolf-moose systems have benefited from such research, developing an extensive body of empirically based theory to base management and research (Orians et al. 1997). Multiple prey systems will be more complex because of the effects of alternate prey. Despite these difficulties, managers will need theory to guide management regarding the effects of predation by wolves on elk populations and the ecological importance of wolves in conservation strategy.

Wolves recolonized the Canadian Central Rockies Ecosystem (CRE, White et al. 1995) during the 1980's from continuous populations to the north (Paquet 1993), denning for the first time in ≥30 years in the Bow Valley of Banff National Park (BNP) in 1986. I focused my research on wolf and elk population dynamics in the Bow Valley using a long-term study spanning 15-years which included the increase in elk populations in the Townsite of Banff and the recolonization of wolves into the Bow Valley. My research benefited from a solid foundation following previous wolf-elk research in the Canadian Rockies (Paquet 1993, Huggard 1993 a,b,c, Weaver 1994, Paquet et al. 1996). This research demonstrated wolves selected elk, and suggested elk herding behavior may be a factor that lead to this selection. Population consequences of selection for elk and effects of herding are uncertain, but suggest a greater impact on elk than expected in solitary prey systems (i.e., moose-wolf). Alternatively, in multiple prey systems, wolves could switch to alternate prey at lower elk densities, reducing the impact of wolves on elk populations. The combination of factors affecting elk population dynamics in BNP include wolf predation, human-caused mortality, variation in climate, winter severity, forage availability, and elk density itself. Understanding how predation by wolves fits in with these complex assortment of factors would aid our knowledge of wolf-elk dynamics.

The objective of my research was to examine the role of some of these factors on wolf-elk populations dynamics to gain a clearer understanding of predator-prey ecology to aid management and conservation. I divided my thesis into three chapters on various aspects of wolf and elk population dynamics. In chapter 2, I examined the impact of elk herding behavior on wolf predation. I tested a novel hypothesis that elk herd size may influence encounter rates and attack success of wolves preying on elk living in herds. I then explored the consequences to wolf-elk population dynamics. Finally, I explored the implications of herd size selectivity by wolves on predation risk for individual elk. This exploration of predation risk offered insights into the evolutionary ecology of wolf and elk dynamics (Gavin 1991) that are relevant to current management problems in BNP.

The study of wolf-prey dynamics benefits from a mechanistic understanding of the components of predation (Holling 1959). One of the most important pieces of information to estimate these components of predation is the kill-rate, or how many prey predators kill per unit time. In chapter 3, I developed a robust statistical estimator for wolf kill-rate. With this estimator, I determined the kill-rate and variance in kill-rate for wolf packs in the Bow Valley from 1986 to 2000. I decomposed kill-rates into species-specific and Bow Valley area-specific kill-rates. I then explored factors that affected different species and total kill-rates, and tested a prey switching hypothesis to gain insight into the importance of multiple prey species to wolves in BNP.

Finally, in chapter 4, I used statistical modeling to explain patterns of variation in elk population growth rate in the 15-year data set for the Bow Valley. Wolves differentially recolonized the Bow Valley as a result of human activity, leading to three different zones with varying wolf predation intensity and elk densities. I constructed a set of a-priori candidate models explaining elk population growth rate from mortality factors wolf predation, snow depth, elk density, and human-caused mortality. I selected the best candidate model from each zone to explore factors affecting elk population dynamics in the different zones using an information-theoretic approach to guide model selection and inference. Finally, I compared candidate models across zones taking advantage of pseudo-experimental conditions to determine the effects of differential wolf recolonization of the Bow Valley on elk population dynamics.

I make conclusions about the effects of predation by wolves on elk populations and other components of the ecosystem in human dominated landscapes. I make predictions based on this research as to the nature of wolf and elk population dynamics in multiple prey systems, and make suggestions for future research. I make management recommendations for the management of ecological integrity in BNP based on the theoretical and empirical implications of my research. It is my hope that the ecological information contained herein will be used by managers in BNP and elsewhere where wolves are recolonizing their former range to develop sound science-based management of our remaining treasures of wildlife and wildlife habitat.

Chapter 2. Effects of Elk Herding on Predation by Wolves: Linking Anti-predator Behavior to Population Dynamics.

Introduction

Historically, predator-prey theory focused on the direct lethal effects of predators on prey giving rise to a wide variety of Lotka-Volterra type approaches that ignored the effects of behavior. Behavior was often left out due to the difficulty in parameterizing behavioral effects on predator-prey dynamics. Holling (1959) incorporated the effects of behavior into predator-prey models by decomposing predation into the numeric response (number of predators) and functional response (number of prey killed per predator) of predators to changes in prey density per unit time. Behavioral aspects of predation were accommodated in the functional response, which decomposed into the encounter and attack stage (Holling 1959, Taylor 1984). The encounter stage included search and detection, while the attack stage included pursuit and capture of prey. How different behavioral processes affect the encounter and attack stages of predation is critical to understanding the consequences of behavior to populations (Taylor 1979, Taylor 1984, Fryxell and Lundberg 1998).

Recently, ecologists have begun to bridge the gap between individual behavior and population dynamics in field studies of predator-prey systems. These recent studies described the effects of predator-induced stress on population dynamics including cycles (Ylönen 1994, Hik 1995, Boonstra et al. 1998), compensatory mortality caused by predator induced starvation risk (Schmitz 1998), shifts in habitat and diet use under predation (Werner et al. 1983, Morgantini and Hudson 1985, Bergerud and Page 1987, Huang and Sih 1990, Kotler et al. 1994, Schmitz 1998, Kie 1999), and behaviorally induced trophic cascades (Turner and Mittlebach 1990, Werner and Anholt 1996).

A common response of many prey species to predation is group living or herding behavior (Bertram 1978, Pulliam and Caraco 1984). Herding benefits prey through dilution of predation risk (Hamilton 1971, Bertram 1978) and/or through reduction in individual vigilance necessary to detect predators (Pulliam and Caraco 1984). Testing between the dilution and vigilance hypotheses is confounded (reviewed in Roberts 1996) because both vigilance (Lima and Dill 1990) and individual predation risk (Hamilton 1971) decrease with increasing herd size. Roberts' (1996) review and empirical work (Dehn 1990) suggests reduction in predation risk through dilution is more important, with vigilance reduction occurring secondarily. Herding behavior could also arise due to the spatial distribution of resources (Geist 1982, Fryxell 1991, Gerard and Loisel 1995), foraging benefits (Hirth 1977), or social facilitation (Geist 1982). Although these other factors are important, the fitness costs of predation (i.e., death) exceed those of starvation and social benefits over time if predation risk is relatively high (Abrams 1993), therefore, reducing predation risk may be the main cause for herding.

Linking predation risk and herding to population dynamics has received little attention. Huggard (1993b) used a simple modeling approach and showed the functional response of wolves (*Canis lupus*) to elk (*Cervus elaphus*) density depended on the relationship between elk density and the number of herds. If the number of elk herds increased with density, wolves encountered more elk herds, with potential changes to the functional response that could increase wolf predation rates on elk ([predation rate = (functional response*numeric response)/prey population size], Holling 1959, Taylor 1979. Huggard (1993b) assumed wolf encounter rates and attack success did not vary with elk herd size, yet herd size has been shown to affect the attack success of other mammalian predators. Lions (*Panthera leo*) had higher attack success on the largest and smallest herds of zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), and gazelles (*Gazella* spp., Schaller 1972, Van Orsdol 1984). Attack success of African wild dogs (*Lycaon pictus*) was higher in herds of >200 (31%) compared to herds of 1 (13%), although this was not statistically significant (Fanshawe and Fitzgibbon 1993). Finally, Crisler (1956) suggested wolf attack success increased with the herd size of caribou (*Rangifer tarandus*). Therefore, changes in wolf encounter rates and attack success with prey herd size, mediated by the relationship between herd size and prey density, could affect the functional response of wolves preying on herding prey such as elk.

Predator-prey modeling prior to wolf reintroduction (Fritts et al. 1997) in Yellowstone National Park (YNP), used research on predator-prey dynamics of solitary prey species (e.g., Gasaway et al. 1992, Messier 1994). Drawing on this literature, Boyce and Gaillard (1992) estimated 25% declines of northern Yellowstone elk populations after wolf recolonization. Garton and Crabtree (1992) predicted a 10% decline in elk numbers following wolf recolonization using a similar approach. These models were useful to managers, suggesting high variation was certain in new wolf-elk systems. However, in Banff National Park (BNP), Alberta, researchers documented 50-70% declines in elk in areas recolonized by wolves (Paquet et al. 1996, Woods et al. 1996, chapter 4). One possible reason for differences between models in YNP and observations in BNP could be the effects of elk herding. Population models that do not incorporate behavior of prey may fail to adequately describe predator-prey dynamics (Brown et al. 1999).

We tested whether elk herd size affected predation by wolves during the winters of 1997/98 and 1998/99 in BNP. On the level of an encounter between a wolf pack and elk herd we tested if 1) the sizes of elk herds encountered by wolves were independent of the sizes of available elk herds, and 2) if the sizes of elk herds from which wolves made kills were independent of the sizes of elk herds they encountered. We examined population level relationships between elk density and both the size and number of elk herds to explore consequences of behavior to population dynamics. We compared these herding relationships with and without predation by wolves to examine differences in elk herding behavior. Regardless of how wolf attack success and encounter rates varied with herd size, we expected individual elk to benefit from herding if herding is an evolutionary stable strategy (ESS, Cockburn 1991). Therefore, we constructed a predation risk model to assess how the relative probability of predation for individual elk living in different herd sizes varied with wolf predation in BNP.

Methods

Study Area

BNP is located 120 km west of Calgary, Alberta, in the front and main ranges of the Canadian Rocky Mountains, is 6641 km^2 in area, and is characterized by extreme mountainous topography (1400 m to 3400 m). The climate is characterized by long cold winters with infrequent warm weather caused by Chinook winds, and short, relatively dry summers. Six species of ungulates are available to wolves in BNP: elk, white-tailed deer (*Odocoileus virginanus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). Elk are the most abundant ungulate in BNP, and comprise 40-70% of the diet of wolves (Paquet et al. 1996). Mule and white-tailed deer occur at low density throughout winter elk range, while moose, bighorn sheep, and mountain goats are rarer and spatially separated from wolves in winter.

Vegetation in BNP is divided into the montane, subalpine, and alpine ecoregions. Montane habitats are found in low elevation valley bottoms, 2-5 km in width, and contain the highest quality habitat for wolves and elk in BNP (Holroyd and Van Tighem 1983, Paquet et al. 1996). The montane ecoregion is characterized by lodgepole pine (*Pinus contorta*) forests interspersed with riparian Engelmann spruce (*Picea engelmanii*) – willow (*Salix* spp.) areas, aspen (*Populus tremuloides*) – parkland, and grassland systems. Sub-alpine and alpine ecoregions are comprised of Engelmann spruce-subalpine fir (*Abies lasiocarpa*) – lodgepole forest interspersed with willow-shrub meadow riparian communities, subalpine grasslands, and avalanche terrain, giving way to open shrub-forb meadows in the alpine ecoregion. The primary study area focused on the Bow Valley (between the towns of Canmore in the southeast and Lake Louise in the northwest) and adjacent side valleys (see Fig.1 in chapter 3). Valley bottom elevations range from 1350 m to 1600 m. The Bow Valley is used by more than 5 million visitors per year (Green et al. 1996). Two towns, the national railway and highway system, and numerous secondary roads and other human developments (ski resorts, golf courses) fragment the study area. The two winters of our study included a mild (1997/98) and an average (1998/99) winter, with mean snowpack depths of 30 and 46 cm, respectively (15-year average, 45cm, chapter 4). See Holland and Coen (1983), Holroyd and Van Tighem (1983), and Huggard (1993a,b) for additional details.

Wolf Monitoring

Wolves were captured and radio-collared using modified steel foot-hold traps (toothed and padded No. 4 offset foot-hold traps, Livestock Protection Co., Alpine, TX) with trap transmitters (Advanced Telemetry Systems, Isanti, MN) in the summer months, or by aerial darting from rotary-wing aircraft during winter. From 1997 to 2000, we chemically immobilized 5 wolves using Ketamine-Xylazine, Telazol, or a Telazol-Xylazine mixture under veterinary direction, and then fitted them with a radio-collar (LOTEK engineering, Newmarket, ON). The BNP Cumulative Effects Assessment task force and Canadian Council for Animal Care approved capture protocol. Radio-collared wolves were relocated almost daily from November to the end of April in each year of the study from the ground or air following Mech (1983). Two wolf packs inhabited the study area during the intensive tracking period. The Bow Valley pack numbered 2-4 wolves and ranged west and south of the Townsite of Banff. The Cascade pack occupied the Cascade Valley to the north east of the town of Banff, and numbered 7-18 wolves.

Elk Herd Size Selection

Availability

Two aerial elk surveys were flown in rotary wing aircraft each year using aerial survey protocol developed for Parks Canada by Jacobson and Kunelius (1985). We conducted surveys in January and March of 1998 and 1999 in the Cascade pack territory, and in April 1998, March 1999, and April 1999 in the Bow Valley pack territory. We used a sightability model for elk herd size and habitat cover class developed in Idaho to correct for missed elk on BNP surveys (Samuel et al. 1987, Samuel et al. 1992) because a preliminary sightability model developed in BNP with a small sample size (n=30) was similar to the Idaho models (Appendix A.1). Recent model validation in Montana (Samuel et al. 1992), and model development in Michigan (Cogan and Diefenbach 1998), Wyoming (Anderson et al. 1998), and Washington (McCorquodale 2000), indicate the Idaho sightability model is robust to changes in study area and time of year.

Encounters

Wolves are almost always hunting while traveling (Mech 1970, Peterson 1977), therefore, the number, species, and herd size of ungulate tracks crossed while tracking wolves give an estimate of wolf encounters with prey. We estimated the size of elk herds encountered while tracking wolves by either snow tracking elk or observing nearby elk herds. We used snow tracking to estimate herd size by tracking elk to bed-sites and counting elk beds, and/or by tracking elk herds until they spread out and then counting individual elk tracks. Observations of elk herds close in space (<1 km) and time (≤ 1 day) to the tracking session were obtained opportunistically and/or in conjunction with concurrent radio-collared elk research in BNP (J. McKenzie, pers. comm.).

Kills

We located prey killed by wolves using tracking and radio-telemetry. Systematic criteria were used to evaluate cause of death (e.g., Gauthier and Larsen 1986), and to determine prey species, sex, and age. We determined the herd size of elk killed by wolves in the same manner as for elk encountered by wolves.

Herd Size Classification Error

Estimates of herd size from snow tracking could be subject to error. We determined error by counting the number of elk in observed herds; field personnel who had not seen the herd visited these areas 1-2 days afterwards and estimated the size of the herd using snow tracks. We assumed counts reflected true herd size because herd sizes were relatively small (<30) and we made repeat counts. We subtracted snow tracking estimates of elk herd size from observed herd size within herd size categories to estimate error.

Comparison of Availability, Encounters, and Kills

We compared the distributions of elk herd sizes available, encountered, and killed by wolves in two stages. First, we determined if we could pool herd size distributions of elk available and encountered by wolves across different wolf packs and years. Secondly, we compared encounters to available, and kills to encounters in these pooled samples within herd size categories.

To determine pooled samples, we compared the herd sizes of elk available to wolves for each wolf pack between years (i.e., Cascade 97/98 vs. 98/99) and between wolf packs for a given year (i.e., Bow Valley 97/98 vs. Cascade 97/98) using the two-sample Kolmogorov-Smirnov (K-S) test to test for differences in the continuous distributions of available herd sizes of elk (Sokal and Rohlf 1995). We determined pooled samples for comparing kills to encounters similarly, comparing herd sizes of elk encountered by packs and years.

Next, we compared wolf selection for herd size within these pooled samples. We tested if herd sizes of elk available to wolves were different than the herd sizes of elk encountered by wolves. Next, we tested if herd sizes of elk encountered by wolves were different than the herd sizes of elk killed by wolves. We conducted all tests between availability, encounters, and kills within herd size categories. We determined herd size categories using natural breaks in the distribution of elk herds available to both packs over both years using K-means cluster analysis where we set the number of elk herd size classes from 3 to 7 (SYSTAT 8.0, Wilkinson 1998). We tested for differences within herd size categories using the G-test (Sokal and Rohlf 1995: 698). We calculated the expected frequency of encounters from the observed number of herds available within herd size categories, and the expected frequency of kills from the observed number of encounters. We used the Williams correction (Sokal and Rohlf 1995: 698) to reduce type I error. We pooled the number of herds in a herd size category with adjacent categories when a category had <5 herds in it. When the G-test indicated a difference, we used adjusted standardized G-test residuals [([observed-expected]/ expected)/ standard deviation] to determine herd size categories where differences occurred and the direction of the difference (sensu Haberman 1973). Probability values for the standardized G-test residuals were adjusted to control for experiment-wise type I error (α=0.05/ number of categories, Sokal and Rohlf 1995).

Elk Herd-Density Relationships

We used BNP aerial elk surveys conducted during late winter from 1985 to 1999 (Parks Canada, unpubl. data) to determine the relationship between 1) the number of herds and elk density, and 2) mean herd size and elk density. The Bow Valley was divided into three survey zones, central (42 km^2), eastern (66 km^2), and western (187 km^2, see Fig.1 in chapter 4), which correspond with low, medium, and high wolf density. To test for the effect of wolf presence on herding-density relationships we analyzed relationships separately from elk sub-populations in zones with (western zone, high wolf) and without wolves (central zone, low wolf, see chapter 4 for detailed zone description). We regressed the number of herds against elk density (elk/km^2), and regressed mean herd size against elk density in both zones to determine herding-density relationships with and without wolves. We used R^2 and AIC_c (Burnham and Anderson 1998) to select among linear and non-linear (exponential, logarithmic) regression models.

Individual Elk Predation Risk Model

We developed a model to evaluate the effects of differential wolf encounter and attack success on relative predation risk for individual elk living in different sized herds following Wrona and Dixon (1991). We used two components of predation, the relative probability of encounter (P_e), and relative probability of successful attack (i.e., death, P_d) to assess predation risk (Turner and Pitcher 1986, Lindström 1989, Wrona and Dixon 1991). We defined P_e as the relative risk of encounter for a particular herd size class, measured by the total number of elk herds in a herd size class encountered by wolves divided by the number of available elk herds in that herd size class. We defined P_d as the relative risk of death for an individual elk given an encounter, measured by the total number of elk killed by wolves within an elk herd size class divided by the herd size and the total number of elk herds available (i.e., total number of elk within that herd size class). We estimated wolf predation risk for individual elk living in different herd sizes in BNP during winter using

$$IPR_i = P_e * P_d = \left(\frac{E_i}{A_i}\right)\left(\frac{K_i}{N_i * A_i}\right) \qquad \text{(equation 1)}$$

where IPR_i = relative predation risk of individual elk in herd size i, E_i= number of elk herds encountered in herd size class i, A_i= number of elk herds available to wolves within herd size class i, $K_{i=}$ number of wolf-killed elk within herd size class i, N_i= number of elk in herd size class i, and i = 1 to n, where n equals the number of herd size categories of elk. Because small sample sizes of kills compared to encounters or availability limited within pack comparisons, we grouped data from both packs and years to examine the risk of predation for individual elk, reflecting predation risk over a broad geographic area (approximately ~4000 km^2).

Results

We found elk herds available to wolves in BNP were best broken into five elk herd size categories using K-means cluster analysis; herds of sizes 1, 2-5, 6-12, 13-30, and $\geq$31 elk, which we used in subsequent categorical tests.

Elk Herd Size Selection - Availability

After correcting for sightability bias (Appendix A.1) the majority of elk herds available to wolves in BNP occurred in herds of 1 and 2-5 (83% for Bow valley pack, 62% for Cascade pack, Table 1). The distribution of elk herds available to the Bow Valley pack (2-sample Kolmogorov-Smirnov (K-S) test = 0.69, p=0.72, n=146) and the Cascade wolf pack (K-S test = 1.29, p=0.08, n=142) were similar between years.

However, the herd size distribution of elk available to wolves in the Cascade pack differed from elk available to the Bow Valley pack during both years (K-S test = 1.78, p=0.004, n=274). Therefore, we compared encounters to availability by individual pack, where possible.

Encounters

We recorded 184 encounters with groups of prey (62% elk) during 627 km of tracking in 1997/98, and 237 encounters with groups of prey (48% elk) during 467 km of tracking in 1998/99 (Table 2). Elk were the most abundant ungulate encountered across packs and years (47-65% of all encounters with groups, and 62-91% of all prey encountered). The distribution of herd size classes encountered between years was similar for the Cascade pack (Table 1, K-S test = 1.06, p=0.21, n=81) and the Bow Valley pack (Table 1, K-S test = 1.22, p=0.08, n = 145). However, Cascade pack encounters were different than Bow Valley encounters for both years (Table 1, K-S test = 1.49, p=0.03, n=226).

Kills

We found a total of 77 prey killed by wolves in both winters of the study, of which 52% were elk, 31% were deer spp., and the remainder moose (9%) and bighorn sheep (8%, Table 2). We located 22 elk kills from the Cascade pack and 11 kills from the Bow Valley pack for which we determined herd size (Table 2) in both winters. Small sample size limited our ability to compare kills to encounters between wolf packs and years. Therefore, we compared kills to encounters by individual pack, and then combined across both packs.

Herd Size Classification

We observed 40 elk herds for which we later estimated herd size using snow tracking to test for herd size classification error. We estimated elk herd size within the correct category 80% of the time using snow tracking (Table 3), and within one herd size class in all other cases (Table 3). Because only 50% of herd size estimates came from snow tracks (the other 50% were sightings), and classification error was small, we felt that the effect of this error on subsequent analyses was negligible.

Comparisons of Availability, Encounters and Kills

The herd sizes of elk encountered and those available to wolves (Table 1) in the Cascade pack differed ($G_{adj}=17.2$, d.f.=3, $P<0.001$), as did the herd sizes of elk killed and encountered (Table 1, $G_{adj}=18.4$, d.f.=3, $P<0.001$). The trend for the Cascade pack was to encounter and kill elk more frequently from larger elk herd sizes than expected (Table 4). Herd sizes of elk encountered and available (Table 1) to the Bow Valley pack were different ($G_{adj}=36.2$, d.f.=3, $P<0.0001$), but the herd size of elk killed and encountered (Table 1) by the Bow Valley pack did not differ ($G_{adj}=2.0$, d.f.=3, $P=0.35$) although sample size of kills (n=11) was small. Despite small differences between encounters and kills for the Bow Valley pack, the trend in differences were similar to the Cascade pack (Table 4). Differences between packs were primarily due to differences in availability (Table 1); trends in encounters and kills were similar for both packs. Therefore, we pooled packs and years. The herd size of encountered elk and those available ($G_{adj}=35.5$, d.f.=3, $P<0.0001$), and the herd size of elk killed and encountered ($G_{adj}=24.0$ d.f.=3,

$P<0.0001$) by wolves from both packs differed (Table 1), and wolves encountered and killed elk in larger herds more than expected (Table 4).

Elk Herd-Density Relationship

We were unable to distinguish between linear and exponential or logarithmic models (Appendix A) for the regression of mean herd size and elk density or number of herds and density in either Bow Valley zone. Therefore, we adopted linear models for these herding relationships. The number of herds increased linearly with elk density (Fig. 1a) but mean herd size did not depend on elk density (Fig. 1b) in the low wolf density zone (central). In the high wolf density zone, both the number of elk herds (Fig. 1c) and mean elk herd size increased linearly with elk density (Fig. 1d).

Individual Elk Predation Risk Model

The relative risk of encounter ($P_e=E_i/A_i$, equation 1) peaked in intermediate herd sizes of 13 to 30 elk (Fig. 2a). The relative risk of death for elk given an encounter ($P_d=K_i/N_i*A_i$, equation 1) also increased in these intermediate herd sizes of elk (Fig. 2a). Combined, the relative risk of predation for individual elk peaked in intermediate herd sizes and was lowest at small and large herd sizes (Fig. 2b).

Discussion

Wolves encountered large elk herds more than expected based on availability (Table 4), and given an encounter, made more kills than expected based on encounters in larger elk herds (Table 4), similar to a wide variety of other predators (Schaller 1972, Van Orsdol 1984, Morgan 1985, Lindström 1989, Fanshawe and Fitzgibbon 1993, Krause and Godin 1995, Connell 1999). Although sample size restricted our ability to directly compare kills to encounters within the Bow Valley pack, these small samples constitute a large proportion of the total elk kills made by the Bow Valley pack during these winters (estimated 34% of all kills during the winter, chapter 3). The trend for wolves to select larger elk herds to encounter and from which to make kills reflected patterns of wolf predation over a large geographic area (approximately ~4000 km^2).

Increased encounter rates and attack success on large elk herds could arise from a number of processes. Detection probability may increase with increasing herd size for olfactory predators (Triesman 1975) such as wolves, increasing encounter rates. Large herds may be more predictable in their location, especially in mountainous terrain, increasing encounter rates of wolves (Huggard 1993b). Attack success may increase in large herds because they are statistically more likely to contain weak or sick individuals (Bertram 1978). Large elk herds are frequently mixed cow-calf herds, and increased vulnerability of elk calves to wolf predation during winter is well known (Carbyn 1983, Huggard 1993c, Weaver 1994), potentially contributing to increased wolf attack success in large herds.

Individual Predation Risk and Life-History of Elk

If encounter rates and attack success increased with increasing elk herd size, why herd at all? Using our predation risk model, we showed individual elk have a lower risk of predation in small and large herd sizes (Fig. 2). In large herds, encounter rates and attack success increased, but this increase was offset by the effects of dilution (1/herd size). In smaller elk herds, lower relative encounter rates and attack success by wolves (Fig. 2) reduced predation risk. Intermediate sized elk herds were encountered and wolves had higher attack success than small herds, yet herd size was not large enough to reduce predation risk through dilution. Thus, individual elk reduced predation risk through a strategy of either 1) diluting predation risk by living in large herds, or 2) living in small herds that had lower encounter rates and attack success.

Ungulates adopt a variety of strategies to reduce predation risk that shape life-history (Bleich et al. 1997, Kie 1999, Kie and Bowyer 1999, Berger and Gompper 1999). Predation risk that peaks in intermediate herd sizes could act as disruptional selection in ungulate life-history evolution, selecting individual elk that adopted a strategy of either living in small or large herds to maximize individual fitness. Predation by wolves may therefore link predation risk to patterns of sexual segregation in elk (Kie 1999). Although we were unable to separate the effects of elk sex on wolf selection for herd size, elk exhibit strong sexual spatial segregation in habitat use (Geist 1982, Unsworth et al. 1998, McCorquodale 2000).

Snow depth and mountainous topography could effect elk predation risk through sexual segregation. Male elk separate from female elk, often living in small groups that winter at higher elevations and deeper snow than females (Geist 1982), which could reduce encounter rates with wolves. Given an encounter, male elk may be able to repel attacks by wolves more successfully due to larger body size. Combined, these factors may contribute to male elk adopting the small group size strategy to reduce predation risk during winter. Conversely, elk females with calves are often restricted by snow to lower elevations because of the small body size of calves (Trottier et al. 1983). Given increased vulnerability of female elk and calves to wolves, dilution of predation risk may be their best strategy to reduce individual predation risk. Further, elk may switch between strategies, whether seasonally as observed in migratory elk populations where pre-parturient females often move to high elevation alpine ranges in small groups (Geist 1982), or opportunistically if predation risk is altered across a landscape by humans or other causes (Jedrzrejewksi et al. 1992). Knowledge of the evolutionary ecology of elk herding and predation risk provides an evolutionary framework (sensu Gavin 1991) for understanding the development of management problems such as urban elk.

Wrona and Dixon (1992) described decreasing predation risk for increasing trichopteran larvae group size, and few larvae lived in small group sizes. Using our individual predation risk model (equation 1) with data from Schaller (1972: p 446), we found zebra, wildebeest, and Thompsons gazelle (*Gazella thomsoni*) showed declining individual predation risk as herd size increased (Appendix A.3), and all three species live in large herds (Jarman 1974). Future research on predation risk-herd size relationships is required to determine if the peaked pattern of predation risk we observed in elk is common in other sexually segregating ungulates.

Potential Consequences to Population Dynamics

Mean elk herd size appeared unrelated to elk density in areas without wolves. Living in herds exacts a cost in terms of reduced foraging opportunities through competition with conspecifics (Geist 1982, Hunter and Skinner 1998). Without predation by wolves, elk may be freed from constraints placed on herd size by predation and follow optimal foraging patterns driven by energetic return (Stephens and Krebs 1986).

However, this relationship without wolves could be due the herd size-density curve flattening out at high elk density (Fig. 1b).

In the high wolf density zone, herd size increased with elk density (Fig. 1d). Encounter rates and attack success also increased with herd size (Table 1,4), therefore they would also increase with elk density. In addition, Huggard (1993b) showed the number of elk herds increased with elk density, and wolf encounter rates increased with the number of herds. Because both encounters and attack success increased with herd size and density, predation rates may increase as a result of changes to the functional response. Constraints of handling and search time would ultimately limit increases in predation rates, but kill-rates may approach these upper limits more rapidly in elk than in solitary prey because of these herding relationships. Therefore, wolf predation rates on elk at moderate densities may be expected to be higher than predictions of solitary, non-herding prey models (Boyce 1992, chapter 4).

Comparison of functional responses for wolves preying on solitary and herding prey provides further evidence for this interpretation. Messier's (1994) type II functional response for wolves preying on solitary moose approached an asymptote more slowly than Dale et al.'s (1994) type II functional response for wolves preying on herding caribou. Dale et al. (1994) speculated that wolf efficiency preying on herding caribou is responsible for this steeper response, and showed the attack rate constant (the *a* in Dale et al. 1994 model) is responsible for the difference in the shape of their wolf-caribou functional response compared to Messier's (1994) moose-wolf response. We found that components of the attack rate constant (encounter rates and attack success) change with herd size, suggesting a potential mechanism for Dale et al.'s (1994) steep type II functional response. Research on the shape and components of the wolf-elk functional response will allow further insight into the effects of herding on predation by wolves.

Environmental conditions may also interact with these wolf predation-herding relationships. Herd size of musk-oxen (*Ovibos moschatus*, Heard 1992) and European red deer (Jedrzejewski et al. 1992) increased with increasing snow depth. Preliminary observations in BNP suggest a positive relationship between snow depth and elk herd size (M. Hebblewhite, pers. obs.) which could interact to increase wolf encounter and attack success rates in deep snow winters, contributing to increased wolf kill-rates on elk in deeper snow (Huggard 1993a, Post et al. 1999).

Considering the effects of herding in predator-prey models will provide an opportunity to determine how increased encounter rates and attack success on large elk herds may affect the functional response. This knowledge may help refine predictive models of wolf and elk population dynamics, and could be used to test whether the effects of herding could explain differences between model predictions in Yellowstone National Park (YNP) and observed elk declines in BNP. Broad ecological differences in habitat, prey distribution, and prey density between BNP and YNP could limit generalization of the patterns we report. However, D. MacNulty (University of Minnesota, pers. comm.) suggested that in YNP, herd size may influence wolf predation similarly as in BNP, because the probability of wolves making a kill once a herd is encountered increased with herd size. Despite differences between study areas and methods, similar patterns of elk herd size influencing wolf predation support the important role that herding behavior may play in determining the effects of wolves on elk populations.

Table 1. Percentages of the total elk herds a) available (after correcting for sightability), b) encountered, and c) killed by wolves in the five different herd size classes by the Bow Valley pack, Cascade pack, and both packs combined, during the winters of 1997/98 and 1998/99 in Banff National Park, Alberta.

a) Available

Herd Size	Bow Valley Pack		Cascade Pack		Both Packs	
	Freq.	%	Freq.	%	Freq.	%
1	49	33.5	21	14.8	70	24.3
2 to 5	69	47.3	67	47.2	136	47.2
6 to 12	17	11.6	30	21.0	47	16.3
13 to 30	7	4.8	12	8.5	19	6.6
>30	4	2.7	12	8.5	16	5.6
Sample size	n= 146		n=142		n=288	

b) Encountered

Herd Size	Bow Valley Pack		Cascade Pack		Both Packs	
	Freq.	%	Freq.	%	Freq.	%
1	28	19.3	6	7.4	34	15.0
2 to 5	65	44.8	28	34.6	93	41.2
6 to 12	33	22.8	22	27.2	55	24.3
13 to 30	16	11.0	16	19.8	32	14.2
>30	3	2.1	9	11.1	12	5.3
Sample size	n= 145		n=81		n=226	

c) Killed

Herd Size	Bow Valley Pack		Cascade Pack		Both Packs	
	Freq.	%	Freq.	%	Freq.	%
1	1	9.1	0	0	1	3.0
2 to 5	4	36.4	1	4.5	5	15.2
6 to 12	4	36.4	6	27.3	10	30.3
13 to 30	2	18.2	10	45.5	12	36.4
>30	0	0	5	22.7	5	15.2
Sample size	n=11		n=22		n=33	

Table 2. Species composition of ungulate prey species encountered (number of herds and individuals in brackets) and killed by wolves in the Cascade (CA) wolf and Bow Valley (BV) packs during winter in Banff National Park, Alberta, 1997 to 1999.

	Encounters						*Kills*					
	97/98			98/99			97/98			98/99		
Species	CA	BV	All	CA	BV	All	CA	BV	All	CA	BV	All
Elk	49 (523)	66 (596)	115 (1119)	35 (1278)	80 (346)	115 (1642)	16	4	20	10	10	20
Deer spp.[1]	19 (66)	29 (82)	48 (148)	27 (85)	80 (209)	107 (294)	3	3	6	6	12	18
Moose	7 (8)	12 (16)	19 (24)	6 (7)	1 (1)	7 (8)	5	1	6	1	0	1
Bighorn Sheep	1 (6)	1 (2)	2 (8)	6 (25)	2 (9)	8 (34)	3	1	4	1	1	2
N=	76	108	184	74	163	237	27	9	36	18	23	41

[1] White-tailed deer, mule deer, and unknown deer species.

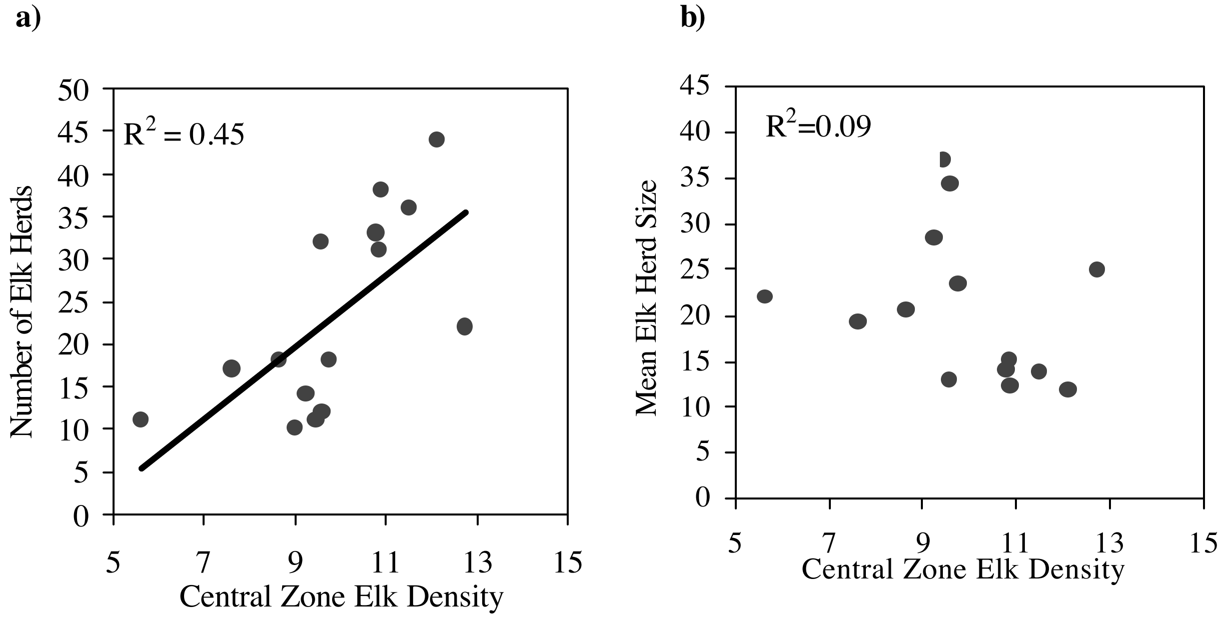
Table 3. Error of snow tracking estimates of elk herd size in BNP during winters 1997/98 and 1998/99.

Herd Size Class	% correct herd size class classification	% within one herd size class	Sample Size
1	80 %	20%	5
2 to 5	57%	43%	7
6 to 12	85%	15%	13
13 to 30	86%	14%	7
>31	87%	13%	8
Mean	80%	21%	N = 40

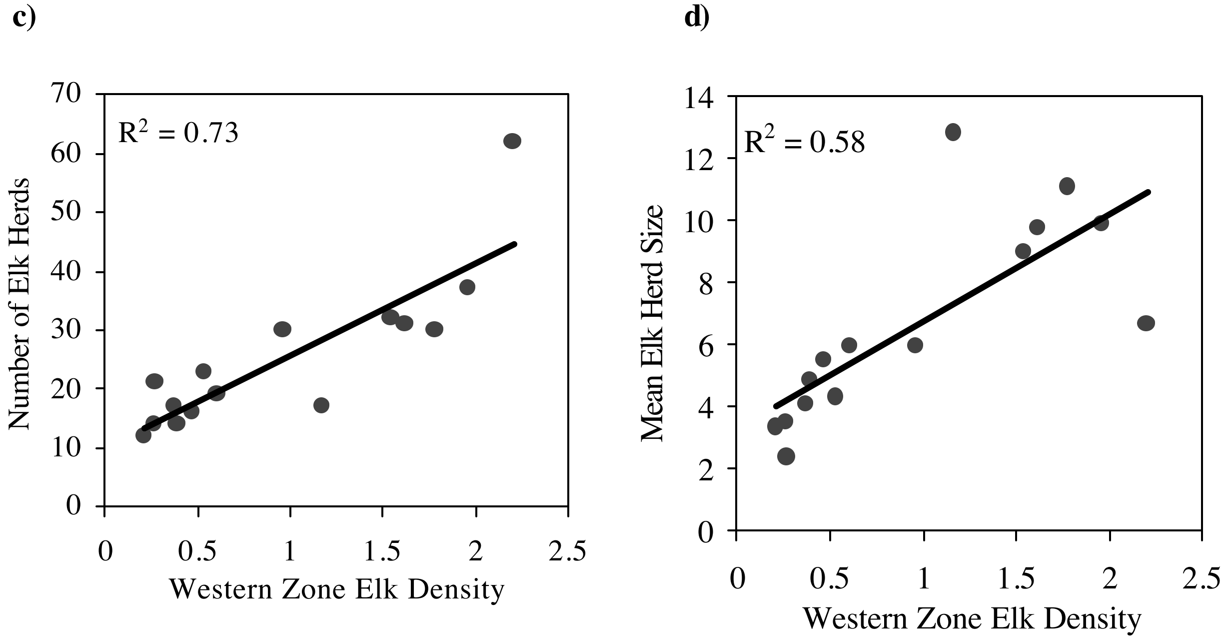
Table 4. Summary of G-test residuals from comparisons of herd sizes of elk killed and encountered by wolves during winter in BNP, 1997 to 1999. Associated p-values and the direction of the difference are presented.

Herd Size Class	Encounters to Availability	Direction	Kills to Encounters	Direction
Bow Valley				
1	p=0.001[2]	Less than	p=0.002	Less than
2 to 5	p=0.216	Less than	p=0.009	Less than
6 to 12	p=0.012	More than	p=0.001	More than
13 to 30	p=0.044	More than	p=0.077	More than
>30	----	----	----	----
Cascade				
1	p=0.034	Less than	----[1]	----
2 to 5	P=0.001	Less than	p=0.011	Less than
6 to 12	p=0.067	More than	p=0.497	More than
13 to 30	p=0.003	More than	p=0.057	More than
>30	p=0.255	More than	p=0.238	More than
Both Packs				
1	p=0.003	Less than	----[1]	----
2 to 5	p=0.053	Less than	p=0.004	Less than
6 to 12	p=0.013	More than	p=0.33	More than
13 to 30	p=0.021	More than	p=0.06	More than
>30	p=0.450	More than	p=0.24	More than

1- Indicates cell frequencies <5, leading to lumping in adjacent cells.
2- Alpha levels were adjusted for experiment-wise error rates with a Bonferoni adjustment (0.05/n cases).



Low Wolf Density



High Wolf Density

Figure 1. Relationships between elk density (elk/km^2) and number of herds (a and c) and mean herd size (b&d) for the central, low wolf density zone (a&b) of the Bow Valley and the western, high wolf density zone (c&d) of the Bow Valley in Banff National Park, Alberta, 1985 to 1999.

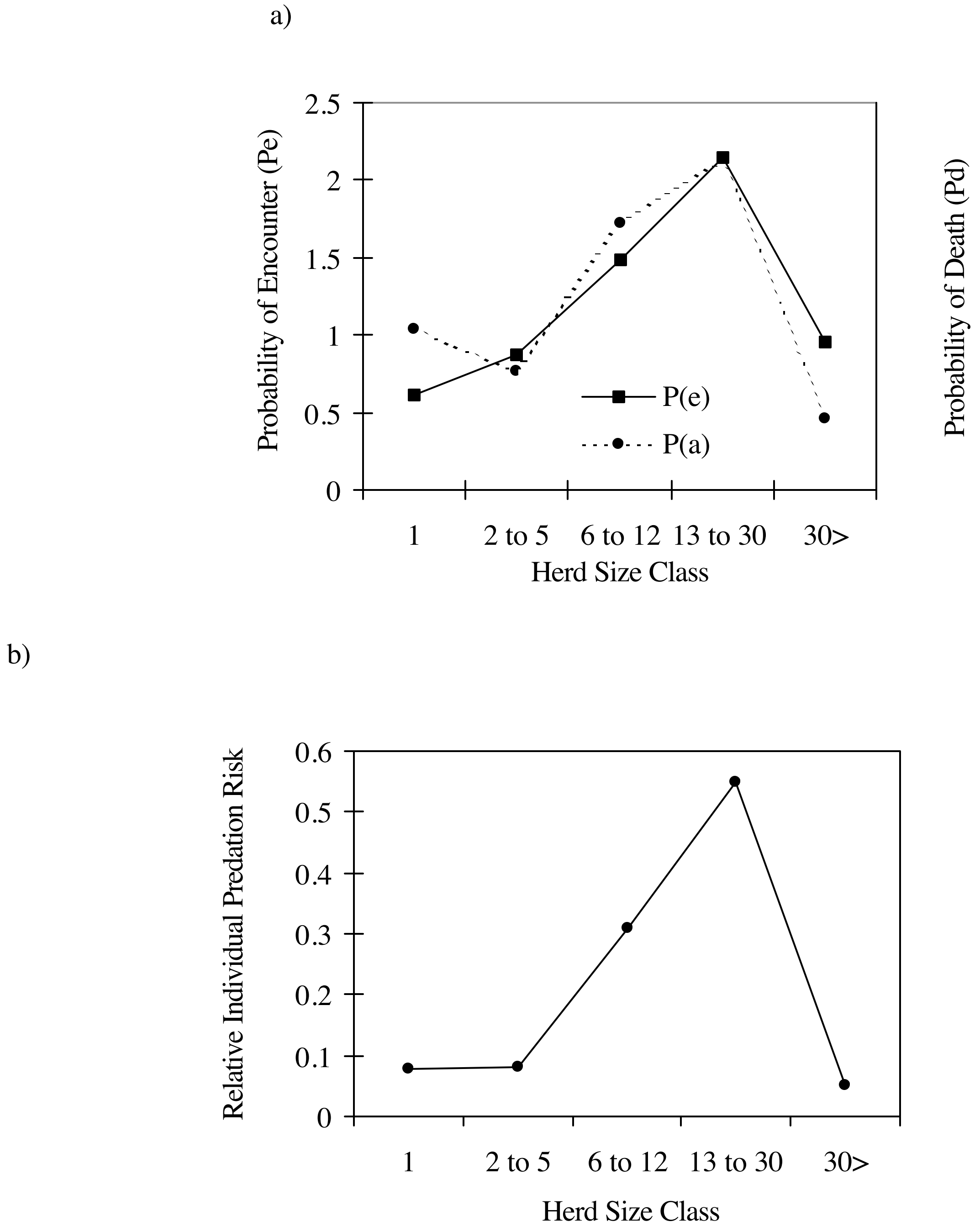


Figure 2. Predation risk of individual elk herd size classes in Banff National Park, 1997 to 1999. The top graph a) partitions individual predation risk into relative risk of encounter (P_e) and relative risk of death given an encounter (P_d), the bottom graph (b) combines these risks for relative individual predation risk of elk.

Appendix A.1 Banff National Park Aerial Elk Sightability Model Development.

Introduction

Bias against detecting small herds on aerial surveys is well known (Caughley 1974). This bias could affect estimates of herd sizes available to wolves. Therefore, I used a sightability model approach for elk herd size and habitat cover class developed in Idaho (Samuel et al. 1987) to correct for this bias during aerial elk surveys in the Bow Valley. Two aerial surveys were flown during the winters of 1997/98 and 1998/99 using aerial survey methodology developed by Jacobson and Kunelius (1985) for Parks Canada. Costs prevented the development of a comprehensive sightability model for elk in BNP. Instead, I developed a preliminary sightability model with two aerial flights in the winters of 1997/98 and 1998/99 using radio-collared elk from a concurrent study (McKenzie, unpubl.data). My objective was to determine differences between a more robust sightability model (the Idaho model in Unsworth et al. 1994) and this preliminary BNP sightability model. If there were no differences, I would use the more robust Idaho model to correct aerial elk surveys for missed elk herds to estimate the herd size distribution of elk available to wolves in BNP for herd size selectivity research (chapter 2).

Methods

I used rotary-wing aircraft equipped with telemetry equipment to determine the number of radio-collared elk herds which were missed on normal aerial elk surveys, following methods described in Samuel et al. (1992). I recorded the herd size and cover class of all elk herds observed and missed on aerial surveys. Variables recorded with all elk observations were herd size and cover class, which was originally collected in 3 categorical variables and later reclassified to match the 7 categorical values of Samuel et al. (1987). I examined the relationship between radio-collard elk herd size, cover class (in 7 classes) and sightability using logistic regression (Hosmer and Lemeshow 1989). The dependent variable was as a dichotomous variable, coded 1 if the radio-collared elk herd was seen and 0 if missed, and independent variables cover class and herd size were associated with each radio-collared elk herd. The logistic regression model used was:

$$Y = \frac{e^{(\beta_0 + \beta_1 X_1 + \beta_2 X_2)}}{1 + e^{(\beta_0 + \beta_1 X_1 + \beta_2 X_2)}} \qquad \text{(equation 1)}$$

where Y = the probability that an elk herd was observed on an aerial survey, X_1 is elk herd size, X_2 is canopy cover coded in 7 categories, and β_1 and β_2 are coefficients of the independent variables X_1 and X_2.

I anticipated limited data would restrict development of a robust BNP sightability model. Therefore, I used forced-entry logistic regression retaining both independent variables in the model, and compared BNP model coefficients to Idaho and Montana model coefficients. To evaluate classification error using the Idaho model in BNP, I used the Idaho sightability model to predict the class (0 or 1) of each radio-collared elk herd observed during surveys in BNP. If the preliminary model did not differ from the Idaho model, and classification error was not large, we would use the more robust Idaho sightability model described by Unsworth et al. (1992) to correct herd size distribution in chapter 2.

Results and Discussion

Previously published models used over 250 data points (Unsworth et al. 1994) to estimate logistic regression models describing elk sightability. I collected only 30 data points during our two sightability flights, 20 herds which were seen, and 10 herds which were missed, limiting development of a robust BNP sightability model. Nonetheless, the preliminary forced-entry logistic regression model indicated that herd size had a positive and measurable effect on sightability (β_1=0.54, S.E.=0.25, P=0.07), and cover class had a negative effect on sightability that was estimated poorly (β_2=-0.44, S.E.=0.42, P=0.4), likely due to small sample size. The intercept estimate for our preliminary model was negative, but poorly estimated and not different than zero (Table A1.1). Compared to the Idaho and Montana models (Table A1.1), parameter estimates did not differ from the BNP model, supporting use of the Idaho model in BNP.

In further support of our use of the Idaho model in BNP, the Idaho sightability model has been validated in Montana (Samuel et al. 1992), and additional model development and refinement has occurred in Michigan (Cogan and Diefenbach 1998), Wyoming (Anderson et al. 1998), and Washington (McCorquodale 2000). These studies indicate the relationships between sightability with herd size and cover class appear robust to changes in study area and time of year. Furthermore, our main objective was to correct the herd size distribution for missed herds, not to correct the number of missed animals. Differences between models generally did not affect the number of herds missed or the herd size category for those missed elk herds as we analyzed effects of wolf selection for elk herd size in categories (chapter 2).

For example, we applied the sightability models for Idaho (Unsworth et al. 1994) and Montana (Hurley 1992) to our aerial survey data from the winter of 1997/98. The same number of herds were ‘missed’ with both models (34), and there were only slight differences in the herd size of the missed herds between the two models. The Idaho model added 137 elk in 34 herds, the Montana model added 164 elk in 34 herds. Finally, the Idaho sightability model correctly classified 80% of the BNP radio-collared aerial elk sample as either seen or not seen based on herd size and cover class. Therefore, I used the Idaho elk sightability model (described in Unsworth et al. 1994) without snow (as snow cover was high) to correct our aerial survey data on elk herd size availability in chapter 2.

Using the Idaho model on aerial elk survey data from 1997 to 1999 indicated approximately 33% of the total number of herds were missed (Table A1.2), and 88% of these herds were in categories of elk herds of 1 to 5 (Table A1.4), confirming a significant bias against detecting small herds. Although our primary interest was in correcting the number of herds missed, we report the corrected numbers of elk from each survey as an estimate of total missed elk (Table A1.3). Aerial elk surveys in BNP underestimated elk population size by 13% (Table A1.3) assuming applicability of the Idaho model to elk in BNP. However, a cautionary note is required regarding the negative intercept term. Although estimated with poor precision, if the negative term persists in further BNP models, this implies sightability for elk is lower in BNP than Idaho, and this effect will be especially prevalent in small herds. While the adjustment to the number of herds missed would not change as much, the percent of the total numbers missed could change substantially. Therefore, the 13% underestimate using the Idaho sightability model should not be applied to BNP elk surveys without further model development.

In conclusion, although the Idaho model did not significantly differ from the preliminary BNP model, the lack of difference may have been due to wide parameter estimates for sightability model parameters. Further model development in BNP should strengthen parameter estimates. By comparison, a relatively robust sightability model developed by Montana Fish, Wildlife and Parks (Hurley 1992) used 60-70 sightability points to develop the model. With 30 points collected for this preliminary model, collection of another 30-40 data points could help stabilize parameter estimates and provide a useful method to estimate the population size of elk in the Bow Valley under a range of sighting conditions. Future work should include more detailed descriptions of cover class and potentially snow cover as independent variables.

Table A1.1: Elk sightability models from Idaho, Montana, and BNP, with parameter estimates and sample sizes used to develop the models. Standard errors for the BNP model are presented for comparison among models. All models are logistic regression models of the form $Y = (e^u/(1+e^u)$ where the dependent variable is the probability of being seen, and u= the linear form of the logistic, $U= B_0+ B_1X_1 + B_2X_2$, where B_1=herd size, and B_2=cover class.

Model	Herd Size	S.E.	Cover Class	S.E.	Intercept B_0	S.E.	N
Idaho [1]	0.296	----	-0.762	----	2.160	----	282
Montana [2]	0.298	----	-0.658	----	1.615	----	63
BNP [3]	0.543	0.255	-0.437	0.419	- 1.919	1.437	30

1- Idaho sightability model first described in Samuel et al. 1987, modified in Unsworth et al (1994). Cover class % was described as a categorical variable in 7 classes.
2- Montana sightability model Hurley (1992) described in Unsworth et al. (1994). Vegetation cover was described in 5% increments above 30% and in 10 % increments below 30%.
3- Forced entry logistic regression model from this BNP. Cover class % was reclassified similar to the Idaho sightability model after originally collected in 3 categorical variables.

Table A1.2: Summary of Idaho sightability model adjustments to the number of herds missed during normal aerial elk surveys in BNP, 1997/98 and 1998/99.

Wolf-Pack Year	Raw # Herds	Corrected # of Herds Using Idaho Model	Raw Proportion Underestimated
1997/98 Cascade	42	63	0.67
1998/99 Cascade	60	80	0.75
1997/98 Bow	37	44	0.84
1998/99 Bow	48	101	0.48
1997/98 Casc/Bow	74	100	0.74
1998/99 Casc/Bow	103	176	0.59
1997/99 Bow Valley	82	142	0.58
1997/99 Cascade	102	142	0.72
1997-1999 Both Packs	177	274	0.65
		Mean underestimate	0.66

Table A1.3: Summary of Idaho sightability model adjustments to the number of elk missed during normal aerial elk surveys in BNP, 1997/98 and 1998/99.

Wolf-Pack Year	Raw # Elk	Corrected # of Elk Using Idaho Model	Raw Proportion Underestimated
1997/98 Cascade	1333	1400	0.95
1998/99 Cascade	1716	1825	0.94
1997/98 Bow	234	250	0.94
1998/99 Bow	292	465	0.63
1997/98 Casc/Bow	1466	1547	0.95
1998/99 Casc/Bow	1895	2165	0.88
1997/99 Bow Valley	367	556	0.66
1997/99 Cascade	3049	3212	0.95
1997-1999 Both Packs	3361	3701	0.91
		Mean underestimate	0.87

Table A1.4. Proportion of the total number of elk herds in herd size classes observed on aerial elk surveys, added by the Idaho sightability model, and combined during winter elk surveys in BNP, 1997 to 1999.

Elk Herd Size Class	Elk Counted	Elk 'Missed'	Combined
1	0.25	0.25	0.25
2 to 5	0.40	0.63	0.48
6 to 12	0.18	0.12	0.16
13 to 30	0.10	0.00	0.07
> 30	0.07	0.00	0.04
Total # of Herds	177	97	274

Appendix A.2. Elk Herd Size Density Relationships

Table A2.1 Model selection criteria for elk herding-density (as independent variable) regression equations, showing linear, logarithmic, and exponential regression equations for each zone and dependent variable, mean herd size or the number of herds. Model selection criteria reported are R^2, P-value, AIC_c and ΔAIC_c (Burnham and Anderson 1998). The model selected by the three model selection criteria is marked with an *.

Dependent Variable and Bow Valley Zone	Model Form	R^2	P-value	AIC_c	ΔAIC_c
Central Zone (No wolf)					
Number of Elk Herds	Linear[1]	0.46	0.006	32.41	0.004
Number of Elk Herds	Logarithmic[2]	0.42	0.009	32.90	0.493
Number of Elk Herds	Exponential[3]	0.47*	0.005*	32.41	0*
Mean Herd Size	Linear	0.10	0.248	32.68	0*
Mean Herd Size	Logarithmic	0.08	0.321	32.86	0.184
Mean Herd Size	Exponential	0.14*	0.169*	32.78	0.096
Western Zone (Wolf)					
Number of Elk Herds	Linear	0.73	0.0005	29.41	1.88
Number of Elk Herds	Logarithmic	0.61	0.001	31.76	4.23
Number of Elk Herds	Exponential	0.78*	0.0005*	27.53	0*
Mean Herd Size	Linear	0.58	0.001	13.88	1.96
Mean Herd Size	Logarithmic	0.69*	0.0005*	11.92	0*
Mean Herd Size	Exponential	0.63	0.0005	14.99	3.0732

1- Linear models are of the form $Y=\beta_0+\beta_1X$

2- Logarithmic models of the form $Y= \beta_0+\beta_1\ln X$

3- Exponential models of the form $Y=\beta_0e^{\beta_1X}$.

Appendix A3. Predation Risk of Ungulates Hunted by Lions in Africa (from Schaller 1972).

Schaller (1972) described number of attacks (encounters) and number of kills for lions (*Panthera leo*) preying on zebra (*Equus grevyi*), wildebeest (*Connochaetes taurinus*), and Thompsons gazelle (*Gazella thomsoni*) in the Serengeti. I used these data in a similar format as the analysis of predation data by wolves on elk in BNP in chapter 2, although I was unable to compare encounter rates to those expected based on availability. I assumed that availability was the same across the three different species, therefore restricting our interpretation of Schallers' data to the effects of differential attack success given an encounter on individual predation risk.

Using the individual predation risk (IPR) model formula developed in chapter 2, I determined IPR using the formula:

$$IPR_i = P_e * P_a = \left(\frac{E_i}{A_i}\right)\left(\frac{K_i}{N_i * A_i}\right) \qquad \text{(equation 1)}$$

Where parameters are defined similarly to Hebblewhite (chapter 2). Table A3.1 describes the data we used to determine patterns of predation risk from Schaller (1972). Using these data, I developed individual predation risk models for the three ungulate species (Figure A3.1).

Literature Cited

Schaller, G. 1972. The Serengeti Lion. University of Chicago Press, Chicago.

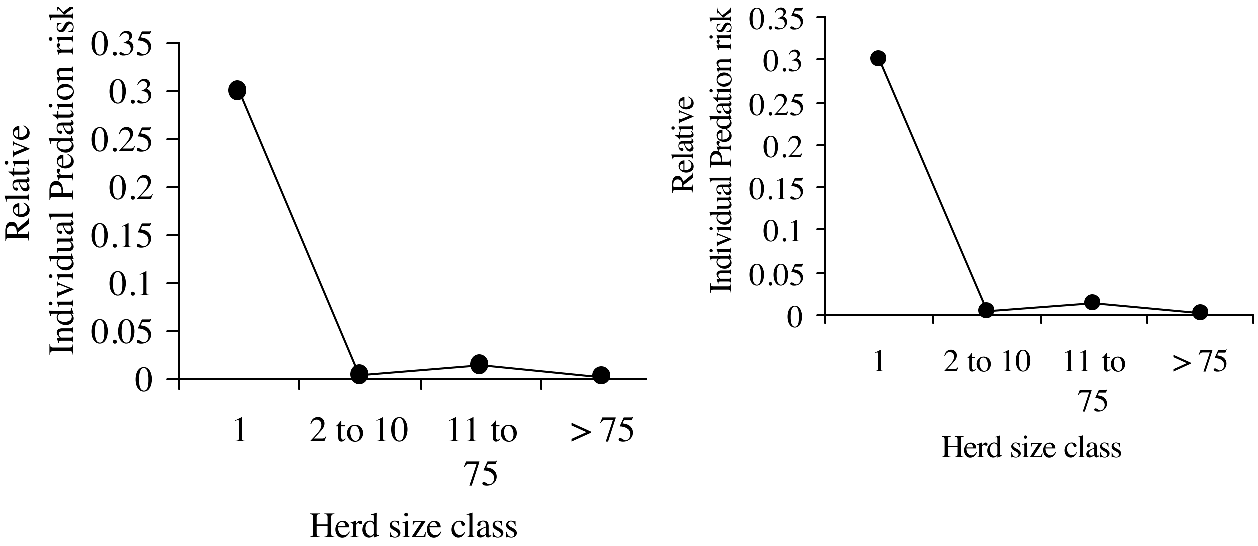
Table A3.1 Proportion of total Gazelle, Wildebeest, Zebra herds a) encountered and individuals b) killed by lions in 4 different herd size classes for the Bow Valley pack, Cascade pack and both packs in BNP, 1997/98 and 1998/99.

a) Number of Lion Hunts

Herd Size	Gazelle		Wildebeest		Zebra	
	Freq.	%	Freq.	%	Freq.	%
1	64	0.15	19	0.33	5	0.13
2 to 10	164	0.39	8	0.14	1	0.03
11 to 75	165	0.40	11	0.19	26	0.68
>75	24	0.06	20	0.34	6	0.16
Sample size	417		58		38	

b) Number of Kills

Herd Size	Gazelle		Wildebeest		Zebra	
	Freq.	%	Freq.	%	Freq.	%
1	33	0.29	47	0.39	60	0.44
2 to 10	21	0.19	13	0.11	21	0.15
11 to 75	25	0.22	9	0.08	23	0.17
>75	33	0.29	50	0.42	33	0.24
Sample size	112		119		137	


a) Wildebeest

b) Thompsons Gazelle

c) Zebra

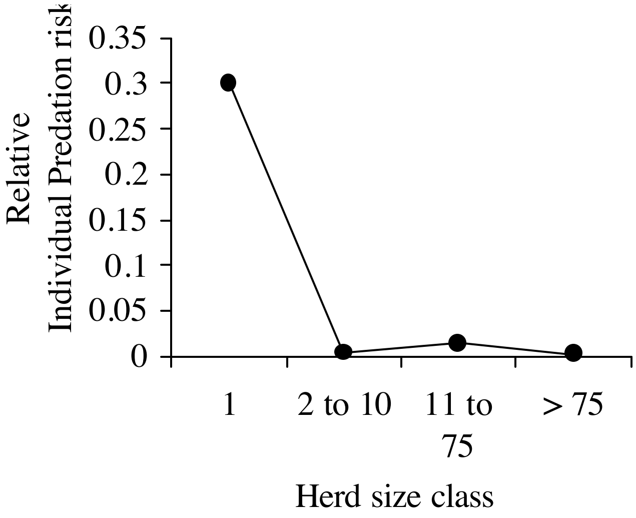


Figure A3.1. Herd size- specific Individual predation risk models for a) wildebeest, b) gazelle, and c) Zebra preyed upon by Lions in the Serengeti of Africa, data from Schaller 1972.

Chapter 3. Estimating wolf kill-rates in a multiple prey system in Banff National Park.

Introduction

Recent recolonization of wolves (*Canis lupus*) across western North America through dispersal (Boyd and Pletscher 1999) and reintroduction (Fritts et al. 1997) is restoring the wolf to ecosystems with multiple prey species. The dominant ungulate in many of these ecosystems is elk (*Cervus elaphus*). Determining the impact of predation by wolves on elk populations is important to test the ecological importance of wolves as keystone, indicator, and/or umbrella species (Estes 1996, Terborgh et al. 1999). In addition, the impact of predation by wolves on harvested elk populations may lead to conflict between recolonizing wolves and hunting by humans (Boyce 1992, Kunkel and Pletscher 1999, Ballard et al. 2000). Wolf predation can limit, and even regulate, populations of moose (*Alces alces*), caribou (*Rangifer tarandus*), and white-tailed deer (*Odocoileus virginianus*, Gauthier and Theberge 1986, Messier 1991, Gasaway et al. 1992, Seip 1992, Messier 1994, Boertje et al. 1996, Ballard et al. 1997, but see Boutin 1992). However, little research has been conducted in wolf-prey systems with multiple species of prey in North America due, in part, to wolf extirpation where multiple prey species are common (Young and Goldman 1944). Predicting the impact of wolves on elk is difficult as quantitative analyses of wolf-elk dynamics have received scant attention.

Elk are the primary prey of wolves in many multiple prey systems, and are often the preferred prey when available (Carbyn 1983, Huggard 1993b, Weaver 1994, Jedrzejewski et al. 2000, but see Kunkel et al. 1999). The consequences of wolf preference for elk to population dynamics is complex due to prey switching (Oaten and

Murdoch 1975, Patterson et al. 1998), alternate prey increasing predator density at low primary prey density (Messier 1995b), spatial distribution of multiple prey species (Iwasa et al. 1981), and differential encounter rates across species (Huggard 1993b). Holling (1959) divided predation into the numeric (number of wolves as a function of prey density) and functional responses (number of prey killed per predator as a function of prey density). Understanding the components of predation in multiple prey systems would provide a theoretical basis for management similar to the large body of predator-prey theory that guides management in wolf-moose systems (Orians et al. 1997).

In multiple prey systems, understanding predator-prey relationships for the primary prey will generate predictions about population dynamics for the entire system (Messier 1995b). If wolves switch between primary and alternate prey disproportionate to primary prey abundance, then the functional response for the primary prey species would be sigmoid or a type III response (Oaten and Murdoch, 1975). Sigmoid functional responses result in low kill-rates at low primary prey density, switching to disproportionately high kill-rates at higher densities because wolf densities depend more on alternate prey species at low primary prey densities (Holling 1959). Alternatively, if wolves select primary prey species in proportion to their abundance, the functional response for primary prey is more likely to be a constantly declining function of prey density, or a type II response. Type II and type III functional responses imply different population dynamics, and have different management and ecosystem implications (Orians et al. 1997).

Determining the shape of the functional response curve requires estimating kill-rate across a range of prey density (e.g., Messier 1994). Wolf kill-rate is costly and difficult to estimate, and methods vary across studies. Marshal and Boutin (1999) showed variation in kill-rate limited statistical power to discern functional response relationships. Unfortunately, few researchers have estimated variance in kill-rate (but see Jedrzejewski et al. 2000, Hayes et al. 2000). Kill-rates are also used to evaluate impact of predation on ungulate populations by estimating the number of ungulates killed over some time period and then comparing loss from predation to estimates of recruitment (e.g., Keith 1983, Fuller 1989). However, only Jedrzejewski et al. (2000) incorporated kill-rate variation into evaluating the impact of predation on ungulates.

We studied predation by wolves during the winter in the Bow Valley of Banff National Park (BNP) from 1986 to 2000. We estimated kill-rates (and associated variance) for 23 wolf pack-years in a multiple prey system for individual prey species and geographic zone using an estimator we developed based on statistical sampling theory. We compared our kill-rate estimator to two other published methods. We tested how kill-rates vary by prey species and zone in BNP to examine predation patterns in a multiple prey system with extensive human use. We tested how population density of the primary prey, elk, affected wolf kill-rates. Finally, we tested whether wolves switched from primary prey to alternate prey species as primary prey density declined.

Study Area

Banff National Park (BNP), 6641 km^2 in area, is located in the front and main ranges of the Canadian Rocky Mountains on the eastern slope of the continental divide. The climate is characterized by short, dry summers, and long, cold winters with infrequent warm weather caused by Chinook winds. The primary study area was defined by wolf pack territories and included the Bow Valley and side valleys (~3000 km^2). Topography is extreme in the Canadian Rockies (elevation 1400 m to 3400 m), and approximately half of BNP is rock and ice unusable to wolves and their prey (Holroyd and Van Tighem 1983). Mean snow depth varies throughout the study area, from 50 cm at the town of Banff to 75 cm in Lake Louise, and is higher in side valleys (Holland and Coen 1983). Prey populations in the study area are among the most diverse in North America, including the numerically dominant elk, mule deer (*Odocoileus hemionus*), white-tailed deer, moose, bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos canadensis*). See Huggard (1993b) and chapter 2 for additional details.

Wolf capture and radio-telemetry methods were described in detail in chapter 2. We radio-collared 18 wolves in five different wolf packs which inhabited the study area at different times between 1986 to 2000 (Fig. 1). The Spray Valley pack inhabited the areas southwest of the town of Banff from 1986 to 1992, and the Castle pack inhabited the upper Bow Valley from 1986 to 1991 (Fig. 1). After 1992, the Spray and Castle packs merged to form the Bow Valley pack (Fig. 1). We grouped these packs into the combined Bow Valley pack for analyses. The Cascade pack occupied the Cascade Valley to the northeast of the town of Banff (Fig. 1) from 1991/92 on. During the fall of 1999/2000, the Fairholme pack formed in the central Bow Valley in the areas surrounding and east of the town of Banff (Fig. 1). Before the Spray, Castle, and Cascade packs formed, these areas lacked resident wolf packs for approximately 30 years. Wolf-pack territories ranged from approximately 500 to 2000 km^2 (using 95% minimum convex polygon, Fig.1, Appendix B).

We divided the Bow Valley into three zones (eastern, central, and western) to determine the effects of predation by wolves on elk sub-populations (see chapter 4 for detailed zone rationale). These zones are based on biological differences between elk sub-populations (Woods et al. 1996), and correspond with medium, low, and high relative wolf density (Paquet et al. 1996). The Bow Valley pack territory overlapped closely with the western zone elk sub-population, while the Cascade pack made primary use of the eastern zone.

Methods

Estimating Kill-rate

Researchers commonly use one of two methods to estimate wolf kill-rate. One method uses aerial radio-telemetry to estimate kill-rate as a function of the number of days wolves are relocated from the air on a kill (Mech 1977, Fuller and Keith 1980). Biases in aerial methods include differences in prey handling times affecting probability of locating wolves on a kill, but these biases have been addressed by Fuller and Keith (1980) and Fuller (1989).

The more common approach used in our study uses ground tracking and radio-telemetry to estimate kill-rate in continuous periods (Huggard 1993a, Dale et al. 1995, Murphy 1998, Hayes et al. 2000). Ground methods are often thought to be the most accurate method to estimate kill-rate (Fuller 1989), yet biases have not been addressed. Methods of defining the start and end of a continuous ground tracking period, called the predation period by Hayes et al. (2000), vary across studies. The length of time between kills (kill interval) before and after the sampled predation period is unknown, and researchers assumed including these periods would bias kill-rates. To minimize this presumed bias, Ballard et al. (1997) removed the first day sampled in a predation period, Hayes et al. (2000) ended a predation period if the wolf pack had not been seen for ≥ 3 days, and Dale et al. (1995) started a predation period the day after the first kill and ended the day of the last observed kill. Murphy (1998) and Jedrzejewski et al. (2000) adopted the Dale et al. (1995) method of truncating the predation period to the day after the first kill and the day of the last observed kill to reduce this presumed bias. No quantitative assessment of this assumption has been conducted, and these truncation approaches reduce the amount of information used to estimate kill-rates.

The Ratio Estimator

To determine the impact of predation by wolves on ungulates, the most common measure of kill-rate is kills per day per pack (k/d/p) for calculating the number of prey killed by a wolf pack. Converting kill-rate to per-capita kill-rate in kilograms of prey killed per day per wolf (kg/d/w) allows comparison across studies with different prey species and wolf pack sizes. Therefore, we developed an estimator for either application that addresses some of the problems in other methods.

Consider a sampling design where wolves are continuously monitored during predation periods and all kills are located within each period. Periods where wolves are monitored are interspersed with periods without monitoring, and assuming these periods are distributed at random (we discuss this below), kill-rate (i.e., kills/day) is a ratio variable. When the number of days in each period is a random variable, this design corresponds to a model-based design for ratio estimation (Thompson 1992: 71). If the relationship between the number of days and the number of kills is described by a linear regression through the origin (wolves make 0 kills in 0 days), this relationship can be used to derive kill rate (Thompson 1992: 71) using the fixed intercept regression model $y_i = \beta x_i$, where y_i= the number of kills in period i (or kg of prey killed in period i for kg/d/w), x_i= the number of days in period i, and β = kill-rate. Kill-rate, β, is then estimated by

$$\hat{\beta} = \frac{\sum_{i=1}^{n} y_i}{\sum_{i=1}^{n} x_i} \qquad \text{(equation 1, Thompson 1992: 73)}$$

where i= the predation period sampled, 1 to n, and n = the total number of predation periods sampled. An unbiased estimate for the variance in kill-rate is

$$\hat{\text{var}}(\hat{\beta}) = \frac{N(N-n)}{X^2 n}\left(\frac{(\bar{x}_{s'})(\bar{x}\ )}{\bar{x}_s}\right)\hat{s}_r^2 \qquad \text{(equation 2, Thompson 1992: 73)}$$

where N= total number of predation periods (sampled and unsampled) in the population, n= number of predation periods sampled, X= total number of days in the study period (i.e., 181 days), $\bar{x}$ = X/N or mean number of days in the population of predation periods, $\bar{x}_{s'}$ = mean length in days of unsampled periods, $\bar{x}_s$ = mean length in days of sampled periods, and $\hat{s}_r^2$ expands to =

$$\hat{s}_r^2 = \frac{1}{n-1}\sum_{i=1}^{n}\frac{(y_i - \hat{\beta}x_i)^2}{x_i} \qquad \text{(equation 3, Thompson 1992: 74).}$$

To estimate the total number of kills (Y) made during the total population of days in a winter period (X), use $Y = \hat{\beta}X$, and to estimate the variance in Y, multiply equation 3 by the number of days in a winter period (X). Dividing kill-rate by pack size, and variance by the delta method (i.e., by pack size^2) gives these relationships for per capita kill-rates. Equation 3 incorporates a finite population size adjustment based on the proportion of total periods sampled.

This approach assumes we selected predation periods at random (Thompson 1992). Our ability to track wolves was often dependent on weather conditions for aerial telemetry, and periods without significant snowfall for ground tracking. Random sampling assumes no difference in kill-rates during periods that are difficult for tracking. In our study, because wolves seemed to travel and hunt under all winter conditions, we felt this assumption was reasonable.

Wolf Monitoring

We monitored wolf packs between the winters of 1986/87 and 1999/2000, defined between November 1st to April 30th (181 days, 182 in leap years). We used a combination of radio-telemetry and snow tracking on wolf packs to locate kills and maintain continuous predation periods for as long as possible. We used mean travelling pack size observed on aerial telemetry flights (average number of wolves travelling and feeding together in a winter, Messier (1985) and Dale et al. (1995)) to calculate per-capita killing rates (kg/d/w).

Kill-rates

We estimated kill-rate, and variance, in k/d/p and kg/d/w (see below for calculation of kg of prey killed) for 23 wolf pack-years using the ratio-estimator from predation periods. We divided total kill-rates into species-specific kill-rates for elk, mule deer, white-tailed deer, moose, and bighorn sheep using the number (or kg) of a particular prey species killed per predation period. We similarly divided kill-rates for elk into the three Bow Valley zones (east, central, and west). We used only prey killed by wolves to estimate kill-rate, and did not include prey scavenged by wolves.

We calculated the mass in kilograms (kg) of prey killed (not equal to consumption rates) by wolves in each predation period using mean mass for each species, age, and sex class killed on highways and railways in BNP from 1982 to 2000 (Table 1, Parks Canada, unpubl. data). To reduce effects of seasonal variation in body mass, we used only winter values for young of year age classes, and when sample sizes permitted, for other age classes (Table 1). Occasionally, we were unable to distinguish the species of deer killed by wolves, and in cases of unknown deer, we used mean values for mule and white-tailed deer. Kill-rates in kg/d/w are not corrected for the percent of the carcass consumed by wolves or lost to scavengers.

Comparison of Methods

We estimated the total kill-rate in k/d/p for the 23 wolf pack-years following the methods of Dale et al. (1995) and our ratio estimator described above. We compared kill-rates estimated with the two methods in each pack-year with a paired t-test, using kill-rate in k/d/p (instead of kg/d/w) because wolf pack size and prey species killed were the same for both methods in paired kill-rates for a given year. Kill-rate methods should not be biased with respect to the length of a predation period. We compared methods for this potential bias by testing whether tracking interval length (x_i) affected individual predation period kill-rate (y_i/x_i) using simple linear regression. Finally, to compare the ratio-estimate of variance in kill-rate (k/d/p) with the approach of Jedrzejewski et al. (2000), we derived an unweighted estimate of variance in kill-rate by treating all predation periods equally (i.e., associated with a straight mean kill-rate).

Factors Affecting Kill-rates

We used kg/d/w for analyses of factors affecting kill-rates to control variation in pack size and prey species killed across pack-years. We tested whether kill-rates differed by prey species and whether elk kill-rates differed by Bow Valley zone using analysis of variance (ANOVA, Sokal and Rohlf 1995). We examined relationships among different prey species kill-rates as density of primary prey (elk) in the Bow Valley declined (chapter 4) as a preliminary test of the prey switching hypothesis (Oaten and Murdoch 1975). If wolves switch between primary and alternate prey, total kill-rate should depend on both primary and alternate prey species kill-rate. If wolves primarily kill elk and do not switch to alternate prey at low elk density, total kill-rate should be unrelated to alternate species kill-rate (Patterson et al. 1998). As primary prey density declines, alternate prey species kill-rates should increase if wolves switch to alternate prey (Oaten and Murdoch 1975).

We used Pearson's correlation's (Sokal and Rohlf, 1995) to compare relationships between prey species kill-rates. If relationships between non-elk species did not differ, we grouped prey into primary (elk) and alternate (all other ungulates) categories. We then used simple linear regression to test the relationships between 1) alternate and total kill-rates, 2) elk and total kill-rates, and 3) alternate and elk kill-rates, where the first and second variable correspond to dependent and independent variables, respectively. We examined these relationships by individual wolf pack, and then combined packs where appropriate.

In addition to evaluating relationships among kill-rates, we tested for the effects of primary prey density (elk) on kill-rate using Pearson's correlation between kill-rates (total, elk, and alternate) and elk density in the western and eastern zones (from chapter 4) for each pack. Although both packs made use of areas outside of these zones, trends within the east and west zones reflected general elk population trends elsewhere within their territories (Parks Canada, unpubl. data).

Statistical analyses were conducted using SYSTAT 8.0 (Wilkinson 1998). For ANOVA, we assessed differences between categories using post-hoc Bonferoni multiple comparisons procedures that controlled for experiment-wise error rate. We assessed normality with normal p-p plots, and variance homoscedasticity with Levene's F-test in ANOVA and residual plots in regression analyses. We transformed variables to meet parametric assumptions when underlying distributions were not normally distributed.

Results

Wolf Monitoring

We monitored eighteen radio-collared wolves in five different wolf packs at different times throughout the study for a total of 23 wolf pack-years between 1986 and 2000. We collected 195 predation periods, locating 429 kills made by wolves over 1294 days (Table 2). We tracked packs an average of 8.5 periods per year and periods averaged 7.0 days in length (Table 2). Mean pack size was 6.1 wolves, ranging from 2 to 18 (Table 2). We monitored wolf packs an average of 31% of the winter study period (Table 2). We summarize wolf predation by prey species, age, and sex elsewhere (Hebblewhite, in prep.).

Kill-rates

Wolf kill-rate averaged 0.33 k/d/p (Table 2), composed of an average of 0.23 elk/d/p, 0.04 mule deer/d/p, 0.022 white-tailed deer/d/p, 0.015 moose/d/p, and 0.017 bighorn sheep/d/p (Table 3). The standard error of total kill-rate (k/d/p) ranged from 0.005 to 0.036, with 95% C.I. that ranged from +/- 0.01 to 0.12 k/d/p (Table 2). Across all packs the pooled 95% C.I. was 0.29 to 0.37 k/d/p, or approximately 52 to 67 kills during a 181-day winter period (Table 2). Wolf packs killed an average of 41.8 elk (95% C.I. 34.9 to 48.7), 7.1 mule deer (3.3 to 10.9), 3.9 white-tailed deer (0.6 to 7.3), 2.7 moose (0.5 to 4.9), and 3.1 bighorn sheep (0.5 to 5.6) per winter. Total kill-rates in kg prey killed/day/wolf (unadjusted for the percent edible, eaten, or lost to scavengers) averaged 9.5 kg/d/w, composed of 8.33 kg/d/w of elk (Table 3), 0.39 kg/d/w of mule deer, 0.38 kg/d/w of white-tailed deer, 0.86 kg/d/w of moose, and 0.36 kg/d/w of bighorn sheep (Table 3). See Appendix B.1 for detailed zone and species kill-rates for each wolf pack-year.

Comparison of Kill-rate Estimators

The Dale et al. (1995) method estimated higher kill-rates (0.36 k/d/p, Table 2) than the ratio method (0.32 k/d/p, Table 2, paired t-test, $t_{22,\alpha=0.05/2}= 2.33$, P=0.03). For the ratio method, the slope of the model $k/d/w_i = \beta_0+\beta_1 x_i$, where x_i is period length in days, was not different than 0 (β_1= -0.0007, S.E.(β_1)=0.001, P=0.31). For the Dale et al. (1995)

method, the slope was marginally different than 0 (β_1= -0.002, S.E.(β_1)=0.001, P=0.07), suggesting a negative bias in kill-rate as predation period increased. Finally, the unweighted estimate of kill-rate variance (Jedrzejewski et al. 2000) overestimated kill-rate variance compared to the ratio estimator by approximately 70% (Table 2).

Factors Affecting Kill-rates

Prey Species

Kill-rates in kg/d/w differed among the five prey species (ANOVA, $F_{4,88}$=36.70, P<0.0005, Table 3). Kill-rates of elk were greater than other prey species kill-rates (P<0.0005), while kill-rates for the four alternate prey species were much lower and did not differ from each other (Table 3, all comparisons $P \geq 0.50$).

Bow Valley Zones

Kill-rates of elk in kg/d/w differed between Bow Valley zones (ANOVA, $F_{2,41}$=5.80, P=0.006, Table 3). Central zone kill-rates of elk were lower than the eastern (P=0.004) and western zones (P=0.004). Although there was not much difference between eastern and western zone kill-rates (P=0.19), this was likely due to high variation in eastern zone kill-rates as a result of partial use by wolves (see discussion).

Prey-Switching

Kill-rates of elk were strongly related to total kill-rate for both packs (Table 4). Kill-rates for individual prey species were unrelated to either elk or total kill-rates in both packs (Table 4), therefore we combined alternate prey species. Similar to the individual species relationships, combined alternate prey species kill-rate was unrelated to either elk or total kill-rates for both packs (Table 4). Relationships among prey species kill-rates for both packs indicated similar relationships in correlation analyses, therefore we report only the combined pack relationships in prey switching regression analyses (see Appendix B for individual pack models).

For both packs, kill-rate of elk (kg/d/w) was strongly related to total kill-rate (Fig. 2a, $F_{1,21}$=283.4, r^2=0.93, P<0.0005), but kill-rate of combined alternate prey was unrelated to total kill-rate (Fig. 2a, $F_{1,20}$=2.95, r^2=0.08, P=0.11). Kill-rate of alternate prey was unrelated to kill-rate of elk ($F_{1,20}$=0.39, r^2=0.04, p=0.39) including the outlier for the Cascade pack from 1991/92. Excluding this point resulted in a shallow negative relationship between kill-rates of elk and alternate species (Fig. 2b, $F_{1,20}$=6.18, r^2=0.24, p=0.02). Relationships within separate packs were similar (Appendix B).

Elk Density

Elk density declined substantially in the eastern and western zones since wolves recolonized in the mid 1980’s (chapter 4). Elk and total kill-rate (in kg/d/w) for both packs declined with decreasing elk density within their respective zone (Table 4). Elk density was unrelated to kill-rates of mule deer, white-tailed deer, or combined alternate prey for both the Bow Valley pack or Cascade pack (Table 4).

Discussion

Wolf kill-rates in BNP (mean = 9.5 kg/d/w) were relatively high compared to published kill-rate estimates from other studies. Wolves in Minnesota killed 1.5 to 5.8 kg of prey/d/w (Mech 1977), preying primarily on white-tailed deer. Thurber and Peterson (1993) found wolves killed approximately 6.2 kg of moose/d/w on Isle Royale. Wolves in a multiple prey system in Denali National Park killed a mean of 6.9 kg of prey/d/w (range 4.1 to 12.0 kg/d/w, Dale et al. 1994), ≥90% of which was caribou. Wolves preyed relatively equally on migratory caribou and moose in Alaska, killing an average of 5.3 kg of prey/d/w (Ballard et al. 1997). In Riding Mountain National Park, Carbyn (1983) found wolves preying on elk in a multiple prey system killed a mean of 6.9 kg/d/w, 78% of which was elk. In another multiple prey system in Bialowieza primeval forest in Poland, wolves killed 7.7 kg/day/wolf, 68% of which was European red deer (Jedrzejewski et al. 2000).

The variability in kill-rate methods we reviewed make direct comparisons across studies difficult, nonetheless, our higher kill-rates were likely due to several factors. Kill-rates were unadjusted for the percent of the carcass edible (approximately 75% by mass for moose, Peterson 1977) or the percent of the carcass actually consumed by wolves (approximately 70% in BNP, Hebblewhite, in prep.). Kill-rates were also not adjusted for the percent of the carcass lost to scavengers such as ravens (*Covus corax*), which can consume up to 50% of a moose carcass killed by a pair of wolves (Hayes et al. 2000). Incorporating these factors is necessary to estimate actual consumption rates for wolves in BNP. In addition, kill-rates were higher than would be expected after wolves and elk are sympatric for some time, because wolf kill-rates declined over the recolonization period concurrent with declining elk density (Table 3, chapter 4, see discussion below). Therefore, the kill-rates we present should not be expected to reflect long-term or equilibrium conditions.

In chapter 4 we show that wolf predation and snow depth can limit elk populations. Parks Canada (unpubl.data) estimated approximately 1000 bighorn sheep in the study area, thus the impact of winter wolf predation on bighorn sheep (6-10 killed by both packs per winter) in our study area should be minimal. In the mid 1990's, Hurd (1999) showed low density moose populations (~50 in the study area) were declining due to low adult survival, and predation by wolves was a leading cause of mortality. The relatively higher impact of winter wolf predation (5-8 moose/winter) on these low density moose populations is consistent with these declines. Assessing the impact of wolf predation on mule deer (14-16 mule deer/winter) and white-tailed deer (8-12 white-tailed deer/winter) is difficult because population sizes for these species have not been estimated in BNP.

Kill-rate estimates varied considerably despite intensive monitoring, and pooling estimates of precision across years masked within year variation. For example, in 1996/97, we tracked the Cascade pack for 45% of the winter in 15 periods, and estimated a kill rate of 0.47 k/d/p. Despite this intense sampling effort, the 95% C.I. was 0.40 to 0.54 k/d/p, larger than if we used the pooled variance estimate (95% pooled C.I., 0.43 to 0.50). Despite intensive sampling effort, substantial process variation remained in kill-rates. A sampling effort of ≥25-30% of the winter period in ≥6-8 predation periods stabilized sampling variance in kill-rate estimates (Table 2, Appendix B). Therefore, intense sampling may be required to reliably estimate wolf kill-rates.

The Dale et al. (1995) kill-rate method estimated higher (8-9 more kills per winter) kill-rates than our method (Table 2). This was likely due to the relationship between the number of days between kills (kill interval) and probability of ending a predation period during wolf tracking. The probability of ending a predation period increases with longer kill interval due to weather, wolf movements, or reaching the end of a pre-determined sampling protocol. By excluding the periods before and after the first and last kill, the Dale et al. (1995) method excluded long intervals without kills, overestimating kill-rate. Reducing the sampling period length in this manner would also increase sampling variation associated with kill-rates. In addition, we found a negative bias in kill-rate with increasing predation period length using this method. In summary, we recommend the ratio method for estimating kill-rate because the ratio method included longer kill intervals between kills than the Dale et al. (1995) method, it showed no evidence for bias with interval length, and has statistical properties based on sampling theory.

Factors Affecting Wolf Kill-rates

Prey Species

Carbyn (1983), Huggard (1993a), and Weaver (1994) reported that elk dominated the diet of wolves in the Canadian Rockies, similar to our results. Kill-rates of elk were much higher than kill-rates of other prey, which did not differ. Kill-rates were ranked elk >> mule deer ≥ white-tailed deer > moose ≈ bighorn sheep, similar to Weaver's (1994) review of North American wolf-elk studies.

Human Disturbance

Human use was the highest in the central zone surrounding the town of Banff and associated urban infrastructure (Green et al. 1996). Lower kill-rates of elk occurred despite much higher densities of elk in this zone (chapter 4) because of the negative relationship between wolf and human use (Paquet et al. 1996). Human use levels were similar in the eastern and western zone (Green et al. 1996), yet eastern zone kill-rates were lower than western zone kill-rates (Table 3). The Trans-Canada Highway (TCH) bisects the eastern zone, which was fenced to reduce highway-caused wildlife mortality (chapter 4) before the Cascade pack recolonized the area. Fencing created a barrier to movement for this wolf pack (Fig.1 in chapter 4, Duke et al. in press) which failed to use wildlife crossing structures to access the south side of the TCH over an 8-year period. Therefore, habitat fragmentation caused by the TCH is likely the main reason why eastern zone kill-rates of elk were lower than the western zone.

Reduced predation by wolves has been linked to increased elk population growth and survival (chapter 4, Woods et al. 1996, McKenzie, in prep.). Increased elk density in the central zone had cascading effects on the ecosystem. These effects include increased elk herbivory on riparian willow (*Salix* spp.) and trembling aspen (*Populus tremuloides*, Nietvelt 2000, White and Feller 2000, White 2001), and indirect and exploitative competition with moose (Hurd 1999), beaver (*Castor canadensis*), and riparian passerines and amphibians (Nietvelt 2000). Although a quantitative test of whether wolves are a keystone species (Menge et al. 1994, Power et al. 1996) has not been conducted, this indirect evidence suggests a causal mechanism of human disturbance altering wolf distribution, with associated cascading effects to lower trophic levels. Future research should test this hypothesis.

Reducing elk populations for public safety and ecological restoration objectives within the central zone is an important management issue in BNP (Parks Canada 1999).

Recent formation of the Fairholme pack during 1999/00 increased kill-rates within the central zone (Table 3). Higher wolf kill-rates for elk in the central zone will limit elk populations (chapter 4). Human-caused mortality is an important factor affecting wolf population dynamics in BNP (Paquet et al. 1996), and human infrastructure has restricted wolf use of the central zone (Duke et al. in press). Therefore, reducing human-caused wolf mortality and human use around the townsite will be critical to reducing elk populations in this zone in the future.

Elk Density

Both total wolf kill-rates and kill-rates of elk declined with elk density over time in BNP. The shape of the functional response of wolves to elk density is the subject of current research (Hebblewhite, in prep.) Regardless of the shape, although the simple correlation between elk density and kill-rates alone cannot imply cause and effect, elsewhere we provide evidence (chapter 4) that wolf predation limited elk population growth rates and size. Reduced elk population size would lead to lower wolf density and kill-rates via well documented wolf-ungulate biomass relationships (Keith 1983, Fuller 1989). We observed high fecundity through multiple litter production in several packs during early wolf recolonization (Paquet 1993, Paquet et al. 1996), suggesting that wolves had abundant prey at this time (Keith 1983, Boertje and Stephenson 1992, Boertje et al. 1996). Kill-rates, body condition, and fecundity of wolves recently reintroduced to Yellowstone National Park (YNP) also appear high (Smith et al. 1999). Therefore, kill-rates, population growth rates, and survival of wolves may be higher early in wolf recolonization than where wolves and prey have been sympatric for some time.

However, human-caused wolf mortality was high throughout the BNP study (Paquet et al. 1996, Callaghan in prep.) precluding simple interpretation of these wolf-elk relationships. Wolf response to prey variation and human-caused mortality are both important factors explaining wolf-elk population dynamics (Keith 1983, Fuller 1989), but determining which factor is more important will be difficult in retrospective analyses, and may not be necessary for park management. The relationship between wolf and prey density (Keith 1983, Fuller 1989) is an ecological process tied closely to Parks Canada's guiding legislation and policies of maintaining ecological integrity (Government of Canada 1988), and human-caused mortality is a human impact on this process.

Prey Switching

We found little support for prey switching by wolves between elk (primary prey) and alternate prey species. Kill-rate of elk (in kg/d/w) explained 93% of the variation in total kill-rate, while alternate species kill-rate was unrelated to total kill-rate (Fig. 2a). Alternate species kill-rate was, however, weakly related to elk kill-rates (Fig. 2b, $\beta_1 = -0.08$, S.E.(β_1)= 0.02), indicating total kill-rates increased very little at low elk kill-rates as a result of this shallow 'switch' to alternate prey (Table 4). These are not strong tests of prey switching because alternate prey densities were not controlled (sensu Patterson et al. 1998). Despite this problem, we suggest wolf kill-rates were closely tied to elk density during our study, and alternate prey species kill-rates were low and essentially constant over a broad range of high elk density (0.21 to 3.55 elk/km^2, eastern and western zone, chapter 4) relative to alternate prey species density. Dale et al. (1994) found little evidence of prey switching in wolf-caribou-moose systems, likely due to wolf selection for caribou. Similarly, strong selection for elk by wolves (Carbyn 1983, Huggard 1993b) may preclude prey switching at the range of elk densities we observed. Alternately, low alternate prey densities (i.e. deer spp., White (2001)) relative to elk in our study area may have precluded prey switching. Future research may highlight the importance of the ratio of elk to deer density for determining the potential for prey switching. However, at the elk and alternate prey species densities in our area of the Canadian Rockies, relationships between wolves and elk will likely dominate wolf-prey population dynamics.

This suggests the functional response of wolves to changes in elk density may be a constantly decelerating function of density, or a type II relationship (Dale et al. 1994, Messier 1994, Hayes and Harestad 2000). Whether predation by wolves is regulatory depends on both the functional and numeric response, especially in multiple-prey systems (Messier 1995b). Given the close relationship between elk and total kill-rates, the y-intercept may be low or close to zero, suggesting regulatory dynamics for wolf-elk systems similar to moose-wolf systems (Messier 1994). Functional responses for alternate prey would be expected to be sigmoid or type III because wolves would switch predation to these species only at high alternate prey densities (Messier 1995b).

Conclusions

Wolf kill-rates are inherently variable, and robust methods must be employed to estimate them. The wide array of methods used to estimate kill-rate is problematic, and following a statistical sampling design improved estimation techniques. In multiple prey systems where elk are the dominant prey species, total wolf kill-rate may depend mostly on elk, and wolves may not switch to alternate prey at low elk densities. Wolf kill-rates may initially be higher following recolonization than when wolves and elk have been sympatric for some time. Humans can affect wolf-prey relationships by excluding wolves through habitat fragmentation and human use. Finally, while we expect analysis of the components of predation will reveal important patterns in wolf-multi-prey systems, it will certainly suffer the same methodological problems that plague the study of wolf-moose systems (Marshal and Boutin 1999). We echo Marshal and Boutin’s (1999) concerns that given low sample size and power, and the high variation we describe in kill-rates, perhaps the best way to infer the effects of wolf predation on dynamics of northern ungulates is to estimate ungulate survival under varying ungulate and wolf densities.

Table 1. Biomass values and sample size (in parentheses) for age/sex classes of ungulates killed on highways and railways in Banff National Park, Alberta, collected from 1982 to 2000.

Age/Sex Class	Species Mass (kg) and Sample Size					
	Elk	Mule deer	White-tailed deer	Deer spp.[1]	Moose	Bighorn Sheep
Adult Female	223	67	58	64	----	63
	(35)[1]	(37)[2]	(16)[2]	(53)[1]		(7)[2]
Adult Male	262	88	81	85	----	78
	(19)[1]	(19)[1]	(12)[2]	(31)[1]		(7)[2]
Adult Combined	237	74	68	72	314	71
	(54)[1]	(56)[1]	(28)[2]	(84)[1]	(7)[2]	(14)[2]
Yearling Combined	139	50	52	51	230	37[1]
	(14)[1]	(15)[1]	(14)[2]	(29)[1]	(5)[2]	(4)[1]
Young of the Year Combined	113	34	38	38	169	29[1]
	(33)[1]	(18)[1]	(4)[1]	(10)[1]	(6)[2]	(6)[1]

1- Determined from winter (Nov 1st to May 1st) sample.

3- Determined from yearly sample due to small sample size in winter.

Table 2. Snow tracking data used to estimate winter kill-rate of wolves in BNP from 1986 to 2000. For each wolf pack-year, the number of tracking periods (N), mean period length in days (x_s), number of days tracked (n), total number of days (X), % of the winter period tracked, number of kills found (y_i), and mean travelling wolf pack size are reported. Total wolf kill-rate in kills/day/pack (k/d/p) and kg prey killed/day/wolf (kg/d/w) were estimated with a model-based ratio-estimator. Kill-rates calculated using the Dale et al. (1995) method are presented for comparison.

Wolf Pack-Year[1]	# of periods (N)	Mean length in days (x_s)	# Days tracked (n)	% winter tracked	# of Kills (y_I)	Wolf pack size	Ratio-estimator kill-rates		Dale et al. (1995) k/d/p	S.E. of (k/d/p)	
							k/d/p	kg/d/w		Unweighted[2]	Ratio[3]
SP 86/87	1	8.0	8	4.4	4	4.0	0.40	18.95	0.313	----[4]	----[4]
SP 87/88	7	7.3	51	28.0	24	5.8	0.47	14.67	0.455	0.052	0.029
SP 88/89	10	5.2	52	28.7	14	5.0	0.29	8.09	0.333	0.041	0.014
SP 89/90	7	13.6	95	52.5	38	4.6	0.40	13.51	0.423	0.013	0.007
SP 90/91	6	7.7	46	25.4	22	6.2	0.48	12.70	0.577	0.080	0.036
SP 91/92	12	6.3	75	41.2	22	6.0	0.29	8.31	0.282	0.078	0.012
CT 90/91	7	6.6	46	25.4	22	5.6	0.48	4.57	0.500	0.051	0.023
BVP 93/94	5	6.0	30	16.6	11	5.3	0.37	10.83	0.200	0.031	0.014
BVP 94/95	11	7.4	81	44.8	19	8.4	0.23	4.05	0.333	0.035	0.010
BVP 95/96	14	6.6	93	51.1	24	5.3	0.26	8.16	0.308	0.026	0.010
BVP 96/97	15	5.5	83	45.9	20	5.9	0.24	6.12	0.438	0.022	0.007
BVP 97/98	7	9.4	66	36.5	5	2.8	0.08	4.61	0.100	0.031	0.011
BVP 98/99	12	5	60	33.1	16	2.3	0.27	14.91	0.462	0.035	0.010
BVP 99/00	8	13.0	104	57.1	12	2.1	0.11	8.70	0.166	0.013	0.005
CA 91/92	4	5.2	26	14.4	9	4.0	0.35	17.52	0.385	0.083	0.032
CA 93/94	7	3.7	26	14.4	8	4.0	0.31	15.27	0.235	0.052	0.018
CA 94/95	8	5.3	42	23.2	13	6.0	0.31	10.55	0.273	0.050	0.019

Table 2. continued.

Wolf Pack-Year[1]	# of periods (N)	Mean length in days (x_s)	# Days tracked (n)	% winter tracked	# of Kills (y_I)	Wolf pack size	Ratio-estimator kill-rates		Dale et al. (1995) k/d/p	S.E. of (k/d/p)	
							k/d/p	kg/d/w		Unweighted[2]	Ratio[3]
CA 95/96	14	7.4	103	56.6	42	8.9	0.41	8.08	0.508	0.019	0.007
CA 96/97	9	8.2	24	13.3	35	13.1	0.46	6.41	0.596	0.053	0.023
CA 97/98	10	6.8	68	37.6	24	15.2	0.35	5.30	0.406	0.025	0.007
CA 98/99	9	4.9	44	24.3	14	12.3	0.30	4.09	0.333	0.037	0.015
CA 99/00	4	6.3	25	13.7	7	6.3	0.28	3.95	0.333	0.033	0.020
FR 99/00	8	5.8	46	25.3	12	2.1[5]	0.26	20.18	0.417	0.039	0.013
$\overline{X}$	8.5	7.0	68.8	31.0	23.7	6.1	0.33	9.98	0.363	----	----
Total[a] or Pooled S.E.[b]	195[a]	----	1294[a]	----	417[a]	----	0.11[b]	5.07[b]	0.0286[b]	----	----

1. Abbreviations are CA – Cascade pack, SP- the Spray pack, CT – Castle pack, FR- Fairholme, BVP- Bow Valley pack, for year, winter 1999/2000 is abbreviated as 99/00.
2. Unweighted variance calculated from unweighted mean kill-rate following Jedzrejewski et al. (2000, see methods) with a finite population size adjustment accounting for % winter tracked (Thompson, 1992).
3. Model-based ratio variance estimate for k/d/p using equation 3 in methods.
4. Only one interval collected for Spray 1986/87 pack.
5. Pack size estimated from snow tracking, no wolves were radio-collared in this pack.

Table 3. Summary of winter wolf kill-rates from both wolf packs combined in kills/day/pack and kg of prey killed/day/wolf for the five prey species, and by Bow Valley zone for elk, in Banff National Park, 1986 to 2000. See Appendix B for detailed data for the 23 wolf-pack years.

	kills/day/pack			kg/day/wolf		
Species / zone kill-rate	$\overline{X}$	Range	Pooled S.E.	$\overline{X}$	Range	Pooled S.E.
Elk	0.23	0.04-0.40	0.025	8.33	1.66-20.18	5.19
Elk – eastern zone	0.12[1]	0.02-0.28	0.036	3.44[1]	0.40-7.71	2.79
Elk- central zone	0.04[1]	0.00-0.20	0.050	1.73[1]	0.0-16.50	3.46
Elk – western zone	0.15[1]	0.03-0.38	0.030	5.99[1]	1.49-16.03	4.33
Mule deer	0.039	0.01-0.12	0.010	0.40	0.15-1.56	0.45
White-tailed deer	0.022	0.01-0.12	0.007	0.38	0.04-1.17	0.32
Moose	0.015	0.01-0.08	0.004	0.86	0.31-6.04	1.35
Bighorn sheep	0.017	0.01-0.09	0.004	0.36	0.04-0.70	0.23

1 – Zone specific kill-rates of elk do not sum to total elk kill-rates because zone specific kill-rates only include years where wolves used a specific zone, while the total elk kill-rate is an average of all wolf-pack years in all zones.

Table 4. Relationships between total kill-rates (kg/d/w), species kill-rates and elk density in the Bow Valley and Cascade wolf packs in Banff National Park, Alberta, 1986 to 2000. Pearsons's correlation coefficients between variables, p-value, and sample size for each pack.

Correlation between	Wolf pack					
	Bow Valley Pack			Cascade Pack		
	r	p	n	r	p	n
Total kill-rates (kg/d/w) and						
Elk	0.99	<0.0005	14	0.92	0.001	8
Alternate prey[1]	-0.26	0.37	12	0.55	0.16	8
Mule	-0.07	0.81	11	-0.18	0.70	6
WTD	0.29	0.45	8	-0.65	0.35	4
Moose	-0.11	0.72	14	0.54	0.35	5
Bighorn Sheep	0.0	0.99	10	-0.51	0.66	4
Elk kill-rates (kg/d/w) and						
Alternate prey[1]	-0.41	0.15	14	0.19	0.66	8
Mule	-0.14	0.63	11	-0.27	0.52	6
WTD	0.17	0.66	9	-0.74	0.25	4
Moose	-0.20	0.50	14	0.47	0.42	5
Bighorn Sheep	-0.07	0.86	8	0.63	0.57	3
Between Elk Density (kg/d/w) and						
Total	0.63	0.02	13	0.81	0.02	8
Elk	0.66	0.014	13	0.90	0.003	8
Alternate Prey[1]	-0.32	0.30	12	0.12	0.28	8
Mule	-0.20	0.52	11	-0.26	0.54	6
WTD	0.33	0.43	8	-0.18	0.83	4
Moose	-0.20	0.52	13	0.20	0.74	5
Bighorn Sheep	0.30	0.44	9	0.90	0.10	3

1- Combined deer species, moose, and bighorn sheep.

2- Elk abundance refers to the number of elk present in the main Bow Valley zone that corresponds to the specific wolf pack. The Bow Valley pack primarily used the western zone, and the Cascade pack primarily used the eastern zone. Using total Bow Valley elk abundance did not change patterns or correlations appreciably.

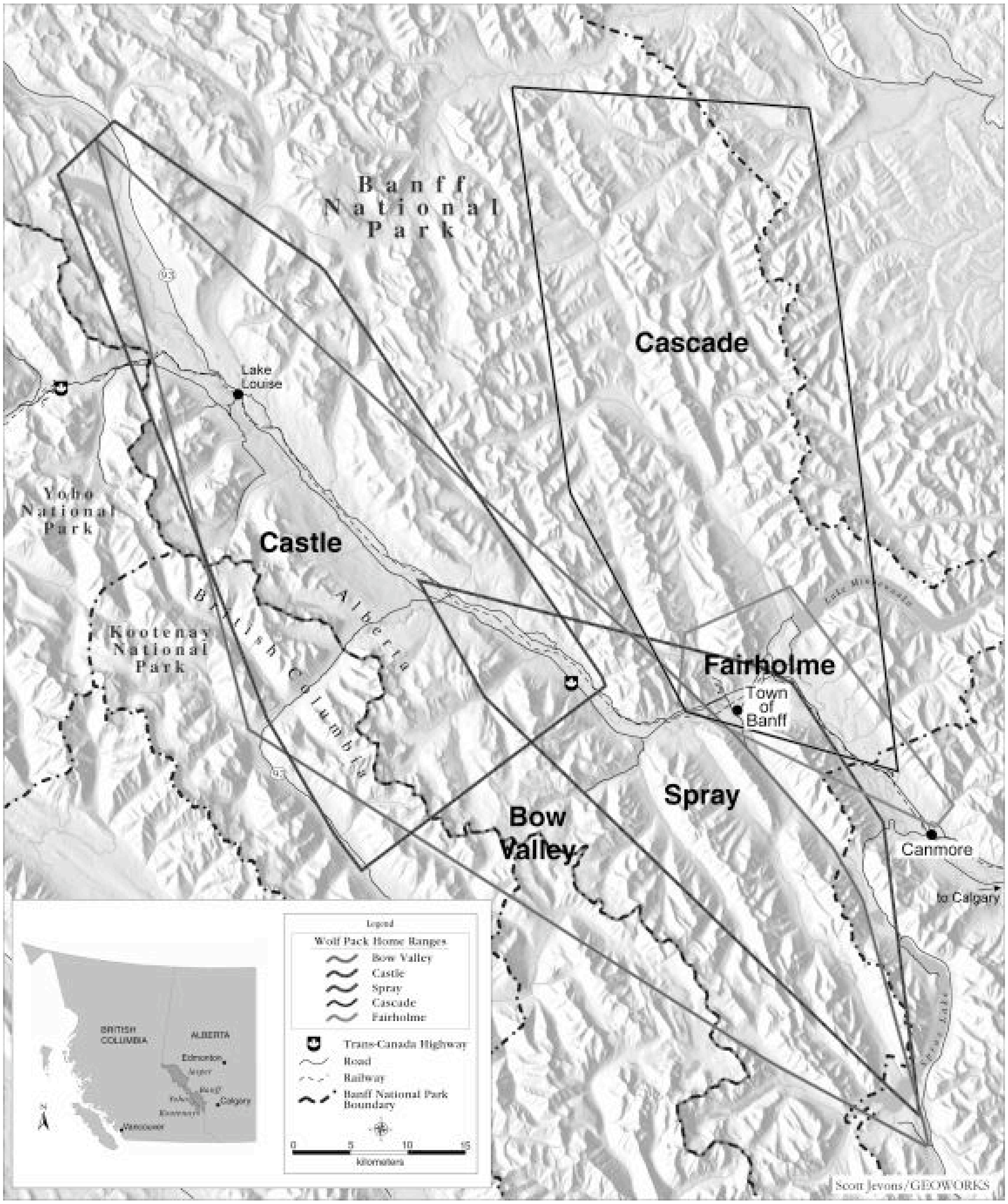


Figure 1. General location of the study area in North America and detailed map of study area showing annual wolf pack territories (95% MCP) for the Cascade, Castle, Fairholme and Spray wolf packs in Banff National Park, Alberta, 1986 to 2000.

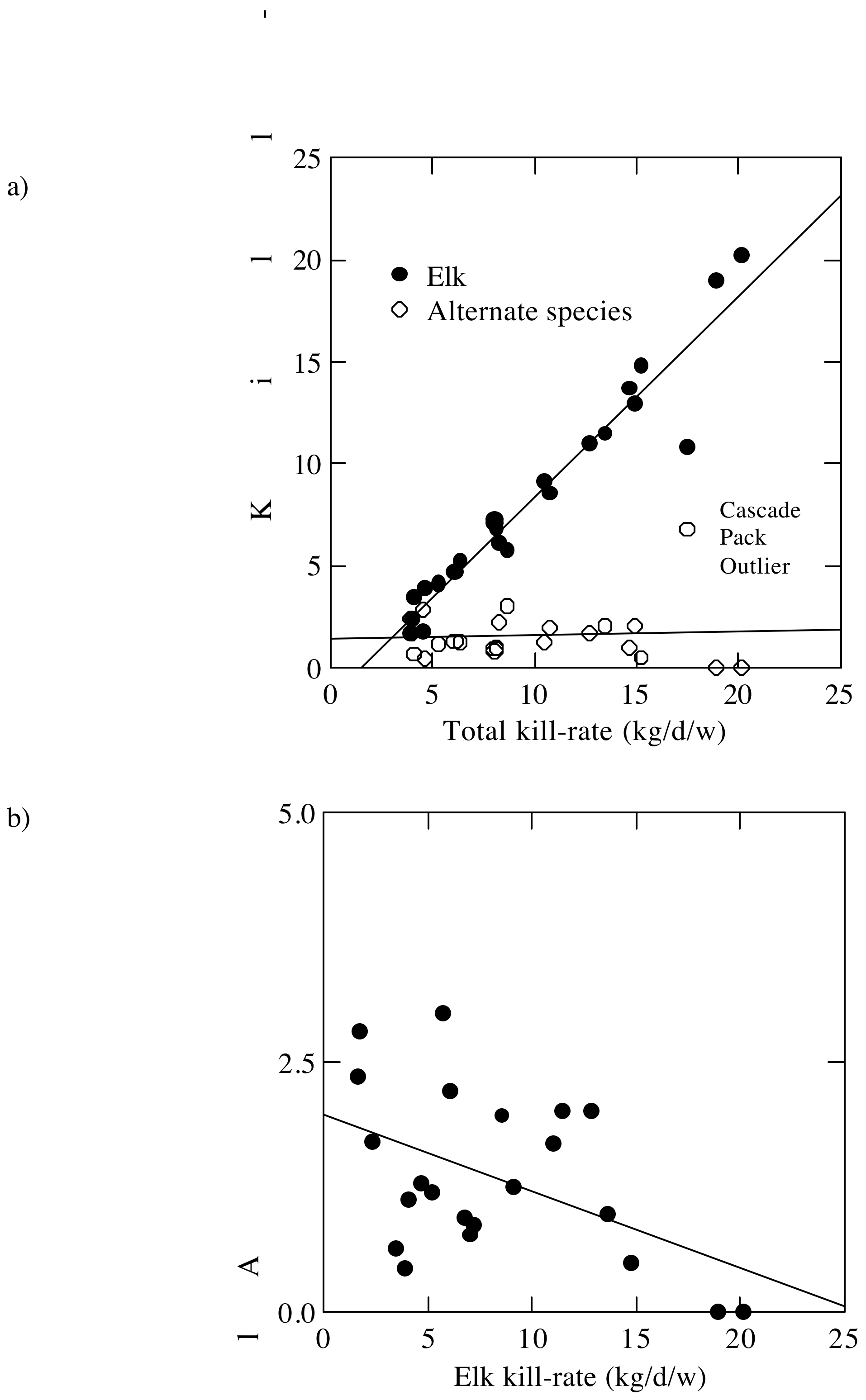


Figure 2. Relationships between a) total kill-rate (k/d/p) and elk (circles) and total kill-rate and combined alternate prey (squares) species kill-rate, and b) elk kill-rate and alternate prey species kill-rate (with the 1991/92 cascade outlier removed), from the combined Bow Valley and Cascade wolf packs in the Bow Valley of Banff National Park, 1986 to 2000.

Appendix B.1. Wolf pack territory sizes, 1986 to 2000

I determined annual cumulative territory size for the Spray, Castle, Bow Valley, and Cascade wolf packs from 1986 to 2000 using the 95% Minimum Convex Polygon (MCP) and 95% Adaptive Kernel home range estimators in CALHOME (Kie et al. 1996). I randomly selected 500 (the maximum allowed by CALHOME) radio-telemetry locations from aerial and confident class '1' ground locations, using a maximum of 1 location per 24-hour period.

Table B1. Cumulative annual wolf pack territory size in km^2 in Banff National Park, Alberta, between 1988 and 2000. Length in years monitored, number of radio-telemetry locations used in estimation (n), 95% Minimum convex polygon, and 95% adaptive kernel home range estimators are presented.

Wolf Pack	Years	n	95% MCP	95% ADK
Spray	1988 – 1993	500	721.2	1010.0
Castle	1988 – 1993	387	1288.0	1644.0
Bow Valley	1994 – 2000	500	1904.0	2641.4
Cascade	1992 – 2000	500	1305.0	1291.0
Fairholme[1]	1999 – 2000	-----	~ 300	N/A

1 – no radio collared wolves in this pack of 2 during this period. MCP home range estimated from snow tracking.

Appendix B.2. Wolf-pack specific prey switching regression models

Table B2. Linear regression models for testing prey switching hypotheses using kg prey consumed per day per wolf, showing parameter estimates, standard errors, and model diagnostics for Cascade, Bow Valley, and both packs combined in Banff National Park from 1986 to 2000.

Pack	Dependent Variable (y)	B_0	S.E.	Independent Variable (x)	Estimate	S.E.	Model Diagnostics R^2	p-value
Both Packs								
	Elk kill-rate	-1.54	0.65	Total kill-rate	0.99	0.06	0.93	p<0.0005
	Alternate kill-rate	1.94	0.38	Total kill-rate	0.06	0.036	0.13	p=0.102
	Alternate kill-rate[1]	1.75	0.35	Elk kill-rate	0.04	0.044	0.04	p=0.39
	Alternate kill-rate[2]	1.98	0.30	Elk kill-rate	-0.08	0.022	0.24	p=0.022
Bow Valley Pack								
	Elk kill-rate[a]	-2.23	0.54	Total kill-rate	1.06	0.050	0.97	p<0.0005
	Alternate kill-rate[b]	1.57	0.59	Total kill-rate	-0.02	0.06	0.04	p=0.85
	Alternate kill-rate[c]	1.85	0.49	Elk kill-rate	-0.02	0.06	0.014	p=0.70
Cascade Pack								
	Elk kill-rate[a]	0.10	1.35	Total kill-rate	0.78	0.13	0.85	p=0.001
	Alternate kill-rate[b]	1.74	0.51	Total kill-rate	-0.07	0.06	0.22	p=0.29
	Alternate kill-rate[c]	1.71	0.40	Elk kill-rate	-0.08	.05	0.32	p=0.18

1- Model including alternate species kill-rate outlier point Cascade 1991/92 (high moose kill-rate)

2- Model without Cascade 1991/92 alternate species kill-rate.

a,b,c – Parameter estimates for the intercept and independent variable did not differ between packs, and so were combined for the both packs analysis for the corresponding prey switching model.

Appendix B.3. Species and Bow Valley Zone Specific Kill-rates

Table B3. Elk kill-rates in kills/day/pack (k/d/p) and kg killed/day/wolf (kg/d/w), with the standard error in k/d/p, in BNP from 1986 to 2000. Total elk kill-rates are divided into zone-specific kill-rates for the western, central, and eastern Bow Valley zones. Elk kills made outside of the Bow Valley are not shown, so the sum of the zone kill-rates do not equal total kill-rates.

Wolf Pack-Year	Total Elk kill-rates			Western Zone kill-rate			Central Zone kill-rate			Eastern zone kill-rate		
	k/d/p	S.E. (k/d/p)	kg/d/w	k/d/p	S.E. (k/d/p)	kg/d/w	k/d/p	S.E. (k/d/p)	kg/d/w	k/d/p	S.E. (k/d/p)	kg/d/w
SP 86/87	0.40	----	18.95	0.38	----	16.03	0.13	N/A	2.93	---[1]	---	---
SP 87/88	0.39	0.029	13.70	0.33	0.025	10.00	0.02	0.007	0.76	0.02	0.005	0.40
SP 88/89	0.21	0.015	7.22	0.10	0.014	3.86	0.10	0.011	2.83	---	---	---
SP 89/90	0.29	0.009	11.50	0.25	0.011	9.89	0.04	0.006	1.09	---	---	---
SP 90/91	0.35	0.037	11.01	0.11	0.019	2.93	0.11	0.016	2.64	---	---	---
SP 91/92	0.20	0.010	6.10	0.19	0.010	5.52	0.01	0.003	0.58	---	---	---
CT 90/91	0.09	0.013	1.76	0.09	0.013	1.76	---	---	---	---	---	---
BVP 93/94	0.30	0.009	8.54	0.27	0.021	6.94	0.07	0.018	1.60	---	---	---
BVP 94/95	0.11	0.006	2.35	0.08	0.005	1.94	0.02	0.002	0.41	---	---	---
BVP 95/96	0.18	0.011	6.79	0.13	0.008	4.77	0.01	0.003	0.28	---	---	---
BVP 96/97	0.12	0.009	4.69	0.04	0.004	1.49	0.10	0.008	2.66	---	---	---
BVP 97/98	0.05	0.010	3.90	0.03	0.007	2.67	0.02	0.009	1.23	---	---	---
BVP 98/99	0.17	0.011	12.90	0.16	0.008	11.31	0.02	0.003	1.59	---	---	---
BVP 99/00	0.05	0.005	5.72	0.04	0.071	4.71	0.01	0.003	1.00	---	---	---
CA 91/92	0.19	0.032	10.80	---	---	---	---	---	---	---	---	---
CA 93/94	0.27	0.020	14.79	---	---	---	0.000	0.000	0.000	0.16	0.016	7.71
CA 94/95	0.26	0.023	9.10	---	---	---	0.000	0.000	0.000	0.12	0.016	3.45
CA 95/96	0.29	0.007	7.07	---	---	---	0.000	0.000	0.000	0.28	0.007	6.79
CA 96/97	0.32	0.021	5.21	---	---	---	0.000	0.000	0.000	0.25	0.020	4.11
CA 97/98	0.24	0.008	4.09	---	---	---	0.09	0.007	1.87	0.03	0.003	0.47

Table B.3. Continued.

Wolf Pack-	Total Elk kill-rates			Western Zone kill-rate			Central Zone kill-rate			Eastern zone kill-rate		
Year	k/d/p	S.E.	kg/d/w	k/d/p	S.E.	kg/d/w	k/d/p	S.E.	kg/d/w	k/d/p	S.E.	kg/d/w
CA 98/99	0.20	0.013	3.46	---	---	---	0.000	0.000	0.000	0.07	0.014	0.92
CA 99/00	0.04	0.021	1.66	---	---	---	0.000	0.000	0.000	---	---	
FR 99/00	0.26	0.013	20.18	---	---	---	0.20	0.015	16.50	0.04	0.006	3.68
$\overline{X}$	0.23	----	8.33	0.14[2]	N/A	5.99[2]	0.04[2]	N/A	1.73[2]	0.12[2]	N/A	3.44[2]
Pooled S.E.	0.025	----	5.19	0.030		4.33	0.05		3.46	0.036		2.79

1- Dashed lines in zone kill-rates indicate wolves did not use that zone during that wolf-pack year.

2- Zone specific kill-rates (k/d/p or kg/d/w) of elk do not sum to total elk kill-rates because zone specific kill-rates only include years where wolves used a specific zone, while the total elk kill-rate is an average of all wolf-pack years in all zones.

Table B4. Alternate species kill-rates in kills/day/pack (k/d/p), kg killed/day/wolf (kg/d/w), with standard error in k/d/p, in BNP from 1986 to 2000. Kill-rates for mule-deer, white-tailed deer, moose, and bighorn sheep are presented. Unknown deer are not included, therefore species totals do not always equal total kill-rates. Dashed lines indicate no kills for that species found.

Wolf Pack-	Mule-deer kill-rate			White-tailed deer kill-rate			Moose kill-rate			Bighorn sheep kill-rate		
Year	k/d/p	S.E. k/d/p	kg/d/w	k/d/p	S.E. (k/d/p)	kg/d/w	k/d/p	S.E. (k/d/p)	kg/d/w	k/d/p	S.E. (k/d/p)	kg/d/w
SP 86/87	0.04	0.009	0.00	----		----	----		----	----		----
SP 87/88	0.06	0.008	0.42	0.04	0.017	0.55	----		----	----		----
SP 88/89	0.03	0.005	0.67	0.02	0.003	0.20	----		----	----		----
SP 89/90	0.02	0.005	0.37	0.03	0.005	0.38	0.01	0.002	0.73	0.03	0.003	0.54
SP 90/91	0.01	0.003	0.18	0.04	0.009	0.44	0.02	0.004	0.59	0.04	0.011	0.47
SP 91/92	0.20	0.014	0.15	----	----	----	0.03	0.005	1.40	0.05	0.010	0.66
CT 90/91	----	----	1.45	0.11	0.012	0.66	----	----	0.00	0.09	0.018	0.70
BVP 93/94	0.05	0.004	0.00	----	----	----	0.03	0.008	1.96	----	----	----
BVP 94/95	0.01	0.002	0.36	0.01	0.001	0.08	0.02	0.004	0.92	0.04	0.007	0.34
BVP 95/96	0.04	0.004	0.18	0.01	0.002	0.11	0.01	0.003	0.64	0.01	0.002	0.00
BVP 96/97	----	----	0.40	0.04	0.004	0.33	----		0.00	0.04	0.003	0.55
BVP 97/98	0.08	0.008	0.00	----	----	----	----		0.00	0.02	0.002	0.43
BVP 98/99	0.03	0.003	1.56	----	----	----	----		0.00	0.02	0.004	0.45
BVP 99/00	0.04	0.012	0.63	0.01	0.003	0.59	0.01	0.003	1.41	0.01	0.001	0.35
CA 91/92	0.04	0.019	0.33	----	----	----	0.08	0.013	6.04	0.04	0.013	0.36
CA 93/94	----	----	0.48	----	----	----	----	----	----	----		----
CA 94/95	0.03	0.003	0.00	----	----	----	0.02	0.009	1.25	----		----
CA 95/96	0.08	0.008	0.16	0.04	0.002	0.26	0.01	0.001	0.34	----		----
CA 96/97	----	----	0.45	0.01	0.003	0.04	0.03	0.004	0.65	0.01	0.002	0.06
CA 97/98	0.05	0.009	0.00	0.01	0.003	0.08	0.06	0.006	1.00	0.01	0.003	0.04
CA 98/99	0.12	0.024	0.26	----	----	----	0.02	0.005	0.31	0.02	0.004	0.05
CA 99/00	----	----	1.19	0.12	0.027	1.17	----	----	----	----		

Table B.4. Continued.

Wolf Pack-	Mule-deer kill-rate			White-tailed deer kill-rate			Moose kill-rate			Bighorn sheep kill-rate		
Year	k/d/p	S.E. k/d/p	kg/d/w	k/d/p	S.E. k/d/p	kg/d/w	k/d/p	S.E. k/d/p	kg/d/w	k/d/p	S.E. k/d/p	kg/d/w
FR 99/00	----	----	0.00	----	----	----	----	----	----	----		
$\overline{X}$	0.039		0.40	0.022		0.38	0.015		0.86	0.017		0.36
Pooled S.E.	0.010		0.45	0.007		0.32	0.004		1.35	0.004		0.23

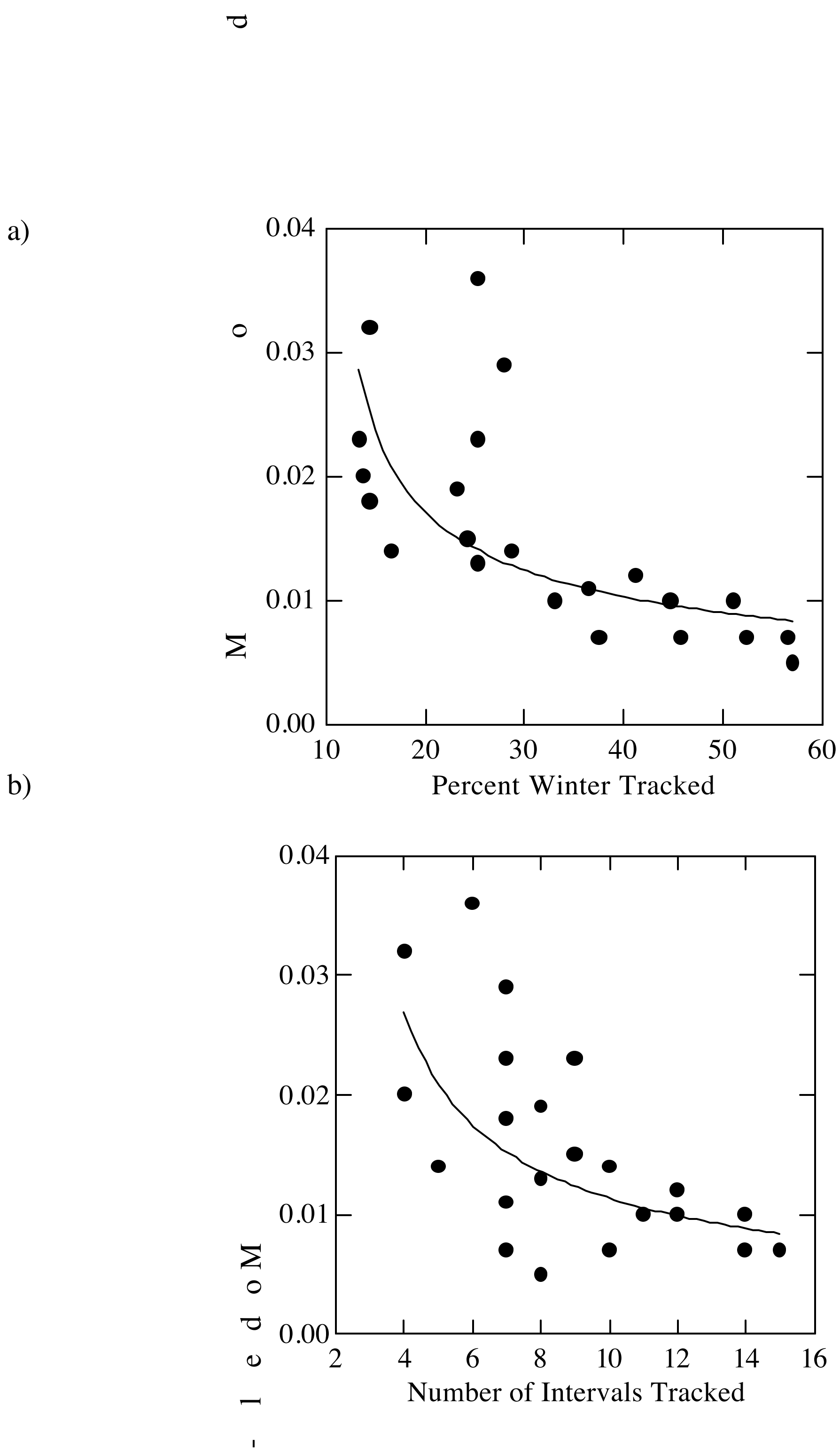


Figure B1. Relationship between the model-based ratio-estimate of the standard error of kill-rate in kills/day/pack and the a) percent of the winter tracked, and b) number of predation periods (intervals) tracked from snow tracking data collected in Banff National Park from 1986 to 2000. The best fitting non-linear curves are a) $Y=0.26x^{-0.88}$, $F_{1,20}=29.7$, $r^2=0.60$, and b) $Y=-0.14\ln(x)+0.045$, $F_{1,20}=11.94$, $r^2=0.37$.

Chapter 4. Factors affecting elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta.

Introduction

Population dynamics of northern ungulates are affected by ungulate density, snow depth, weather, and predation (see reviews in Sæther 1997, Gaillard et al. 1998). Studies conducted in areas without predators emphasize density-dependence and weather as drivers of ungulate population dynamics (Picton 1984, Albon et al. 1987, Clutton-Brock et al. 1987, Merrill and Boyce 1991, Langvatn et al. 1996, Jedrzejewska et al. 1997, Sæther 1997, Singer et al. 1997, Portier et al. 1998, Post and Stenseth 1998, Post et al. 1999, Post and Stenseth 1999, Milner et al. 1999). Increasing ungulate density and severe weather decrease survival, and severe winter weather can interact with density, exacerbating mortality (e.g., Portier et al. 1998, Milner et al. 1999). Adult survival is relatively high and constant, while juvenile survival varies with weather and density, and is often the prime determinant of population growth rate (Gaillard et al. 1998).

Factors affecting population dynamics of northern ungulates are less clear when they are sympatric with predators such as gray wolves (*Canis lupus*), but general patterns are emerging of predation by wolves *limiting* if not *regulating* growth rate and size of ungulate populations (Skogland 1991, Messier 1994, Orians et al. 1997). Limiting factors are density-independent, such as the effects of climate on growth rates, whereas a regulatory factor is density dependent, such as density-induced starvation (Sinclair 1989). Despite the difficulties in applying rigorous experimental design to predator-prey studies (Boutin 1992, Orians et al. 1997, Minta et al. 1999), many researchers have reported wolf predation decreases ungulate survival or growth rate, including some pseudo-experimental wolf controls (Gauthier and Theberge 1986, Gasaway et al. 1992, Hatter and Janz 1994, Boertje et al. 1996, Jedrzejewska et al. 1997, Bergerud and Elliot 1998, Berger et al. 1999, Kunkel and Pletscher 1999, Hayes and Harestad 2000). Many researchers found wolf predation increased with snow depth (Nelson and Mech 1986, Huggard 1993a, Post et al. 1997, Post et al. 1999), indicating predation interacts with weather in its effect on ungulate populations.

Analyses of factors affecting ungulate population dynamics have progressed from simple (Mech et al. 1987) and multiple linear regression (Messier 1991, McRoberts et al. 1995), to accommodate complexities of collinearity, time lags, and autocorrelation in generalized linear modeling of population dynamics (Royama 1992, Post et al. 1997, Portier et al. 1998, Milner et al. 1999). This progression reflects the complexity of these systems, yet methods suffer from two fundamental statistical problems; model selection uncertainty (Burnham and Anderson 1998, Anderson et al. 2000), and the limitations of correlative studies in general (Royama 1992, Boyce and Anderson 1999).

Traditional model selection methods (e.g., stepwise) inadequately address model selection uncertainty and often are poor at selecting the correct model in complex systems (Burnham and Anderson 1998). Sparse data often limits our ability to distinguish among hypotheses in predator-prey research (Marshal and Boutin 1999), yet traditional hypothesis testing only allows consideration of single models (Burnham and Anderson 1998, Johnson 1999, Anderson et al. 2000). Analysis of complex systems such as ungulate population dynamics may benefit from adopting an information-theoretic approach where the philosophy of multiple working hypotheses (Chamberlain 1890) is central.

Problems with correlative approaches in the study of population dynamics are difficult to remedy (Royama 1992, Royama 1996, Boyce and Anderson 1999). Experiments are the best way to tease such factors apart (Underwood 1997), yet in a recent review, Minta et al. (1999) noted applying classic experimental design to predator-prey systems is nearly impossible, and others echoed these sentiments (Estes 1996, Terborgh et al. 1999). The only consistent advice has been to take advantage of natural experiments that provide variation in carnivore and ungulate density, and to compare population processes across this range of densities (Sinclair 1991, Royama 1992, Orians et al. 1997, Minta et al. 1999, Elkington 2000).

Wolves recolonized the Bow Valley of Banff National Park (BNP) during the mid 1980's (Paquet 1993). Paquet et al. (1996) and Woods et al. (1996) suggested wolves were an important factor affecting elk population dynamics after recolonization. Human activity excluded wolves from an area (zone) of the Bow Valley (Green et al. 1996), providing a serendipitous pseudo-experiment to evaluate the effects of different levels of wolf predation on elk population growth rate in different zones. We selected wolf predation, elk density, human-caused elk mortality, and snow depth (as a measure of winter severity) as possible determinants of elk population growth in BNP, and constructed an a-priori set of candidate models using these factors to explain population growth rate. We fit time series data from long-term monitoring of elk and wolf population dynamics from 1985 to 2000 to this set of candidate models. We adopted an information-theoretic approach to guide model selection, using Akaike Information

Criteria (AIC, Burnham and Anderson 1998) to select the best candidate model(s) for each zone. We compared models in zones with and without wolves to determine the effects of differential wolf predation on elk population growth rate. If predation by wolves limits elk population growth rate, we predicted 1) elk populations will decline from pre-wolf conditions in areas with wolves compared to areas without wolves, 2) wolf predation should reduce ungulate population growth rate in areas with wolves, 3) high elk density should decrease growth rate in areas without wolves, 4) snow depth should interact with predation by wolves on elk in areas with wolves to decrease growth rate in deep snow winters, and 5) snow depth should interact with high elk density in areas without wolves to decrease population growth rate.

Study Area

Banff National Park (BNP), 6641 km^2 in area, is located on the eastern slope of the continental divide in the front and main ranges of the Canadian Rocky Mountains, and is characterized by extreme mountainous topography (1400 m to 3400 m). The climate is characterized by long, cold winters and short, relatively dry summers. The primary study area centers on the Bow Valley and adjacent side valleys. Mean snow accumulation in the valley-bottom averages 50 and 75 cm at Banff and Lake Louise, respectively, but is greater in side valleys and higher elevations. Two major towns ($\leq$ 10,000), the national railway (Canadian Pacific Railway, CPR) and highway (Trans-Canada Highway, TCH) system, numerous secondary roads and human development (ski resorts, golf courses) fragment the study area (see Fig. 1, chapter 3). See Huggard (1993 a,b) and chapter 2 for additional details.

Methods

Bow Valley Zones

During winter, elk in BNP are restricted to low elevations of the Bow Valley (Fig. 1, 2, Woods 1991, Woods et al. 1996, McKenzie 2001). Wolf, human, and elk densities vary throughout the Bow Valley (Fig. 1&2, Green et al., 1996, Paquet et al, 1996, Woods et al. 1996), and we divided the area into three zones (eastern, central, and western) that reflected these differences. General patterns of elk mortality and elk and wolf density in the Bow Valley zones are summarized in Table 1. Elk exist in sub-populations corresponding to these three zones, with little permanent migration (<5%) and differing mortality patterns between zones (Woods 1991, Woods et al. 1996, McKenzie 2001). Human use was the highest in the central zone surrounding the Townsite of Banff (Green et al. 1996), excluding wolves (Paquet et al. 1996), and reducing predation on elk (chapter 3). Highway-caused mortality of elk in the central zone declined after TCH fencing was completed by 1990 (Clevenger et al. in press). Wolf predation on elk was higher in the western zone (chapter 3), and elk were exposed to high railway and highway-caused mortality (prior to TCH fencing in 1997). Wolves recolonized the eastern zone in 1992/93; however they used this zone unevenly because of habitat fragmentation caused by the TCH (Fig. 1, chapter 3). Elk are exposed to high human-caused railway mortality in this zone, but highway caused mortality was eliminated following fencing in the mid 1980’s (Clevenger et al. in press).

Wolf Monitoring

We describe capture, radio-collaring, radio-telemetry, snow tracking, and kill-rate methods in detail in chapters 2 and 3. We studied 5 wolf packs from 1986 to 2000 (detailed description and map in chapter 3). The Castle and Spray packs merged to form the Bow Valley pack in 1992/93, and were considered one pack for analysis. The Bow Valley packs made use of the western zone of the Bow valley. The Cascade pack formed in 1992/93, the Fairholme pack in 1999/00. These packs primarily used the eastern and central zones, respectively.

Elk Population Size and Population Growth Rate (r)

We determined elk population size using late winter aerial elk surveys from 1985 to 2000 following methods developed by Jacobson and Kunelius (1985) for Parks Canada. We used raw elk counts from aerial surveys because they have been shown to be similar to previous mark-recapture estimates (Woods 1991). Elk locations on surveys were used to assign elk to zones. We calculated elk density using the area of each of the three survey zones (east, central and west). Survey zone boundaries were delineated by an elevation cut (to exclude rare observations) derived from aerial survey elk sightings and the survey flight line (Jacobson and Kunelius 1985). Elk were located below ~2000 m 99% of the time during winter in the BV (Fig. 2). Therefore, we used this elevation contour to delineate zone boundaries using Idrisi16-GIS (Clark Labs) and a 1:50,000 digital elevation model. The BV zones were eastern zone - 66 km^2, central zone - 44 km^2 and western zone - 187 km^2 in area (Fig. 2), and we calculated winter range elk density (elk/km^2) using these values.

We defined our biological year from May 1st to the following April 30th, approximating the life cycle of elk with aerial survey methods (Fig. 3). We calculated elk population growth rate using the instantaneous or exponential population growth rate, $r = \ln(N_{t+1}/N_t)$. We used exponential growth rate instead of percent change in population size (i.e., lambda) because taking the natural log of lambda reduces statistical dependence between lambda and population size (Royama 1992: 6-7), and is equivalent to differencing time series to produce stationarity required for time series analyses (Royama 1992).

Snow Depth

We estimated mean snow depth during each winter by averaging snow depths measured at 15-day intervals between October 15th and April 30th at the base of Banff Mount Norquay ski resort (© Banff Mount Norquay, 2000) in the central zone (1700 m elevation). Snowfall varied substantially in timing and duration across all winters, and snow depth influences ungulate population growth through its effects on locomotion, foraging, and interaction with predation (Telfer and Kelsall 1984, Hobbs 1989, Huggard 1993a). Therefore, we used mean snow depth to investigate the effects of winter severity on elk population dynamics. We included a SNOW*WOLF interaction in zones with predation (east, west) and SNOW*ELK term in the central zone to test for these interactive effects on growth rate (Appendix C).

Previous researchers described the importance of time-lag effects of snowfall (Post and Stenseth 1999) and cumulative snowfall on ungulate growth and survival (Mech et al. 1987, McRoberts et al. 1995). We tested for time-lags between snow depth and growth rate using cross-correlation function (CCF) analysis to ensure the snow index in our candidate model set was the appropriate measure (sensu Post and Stenseth 1998). Messier (1991) reasoned the r^2 values of the relationship between growth rate and cumulative snowfall should increase over the relevant integration period (1 or more years) if cumulative snowfall was important. Therefore, we examined trends in Pearsons correlation coefficients between population growth rate and the cumulative snow depth over 1 to 3 years to determine the appropriate cumulative period for snow depth.

Human-Caused Elk Mortality

We determined the number of elk killed by humans (on the TCH and CPR) during the winter between November 1st and April 30th of each year and zone from BNP warden service records (Parks Canada, unpubl.data). We used only winter human-caused mortality for comparison to winter wolf kill-rates (see below) to keep time periods consistent. We converted the number of elk killed by zone into a daily winter rate (elk killed/day) to further facilitate comparison to winter wolf kill-rates. We compared human-caused mortality rates (arcsine square-root transformed) between zones using ANOVA. We tested for the overall effect of TCH fencing on central zone growth rate by including a dummy variable for whether the TCH was fenced (0 – TCH not fenced, 1- fenced). No fencing variables were used in the east and west zone because fencing was either present (eastern) or absent (western) for much of the time period, having little time to affect growth rate in a measurable manner.

Wolf Pack Size and Kill-rates

Mean travelling wolf pack size was determined similar to Messier (1985) and Dale et al. (1994, chapter 3). We combined pack sizes when more than one wolf pack used a zone to estimate the total number of wolves using that zone. We estimated zone-specific per-capita kill-rate for elk (elk/day/wolf/zone) from continuous tracking intervals (chapter 3). Kill-rate per pack (total kill-rate) integrates the number of wolves in a zone and their use of that zone (kill-rate). Therefore we multiplied the total number of wolves by the kill-rate (elk/day/wolf/zone) to determine the total kill-rate (elk/day/zone/pack), or the total predation response (Messier 1995b).

Post and Stenseth (1998) reasoned Messier's (1991) analysis of the effects of predation rate (total kill-rate as a proportion of the prey population) on moose dynamics was subject to the problem of lack of independence between variables or spurious correlation (e.g., McCullough (1979): p89, but see Prarie and Bird (1989). Therefore, Post and Stenseth (1998) used wolf density only in their analysis. We tested how total kill-rate affected elk population growth rate, a more informative index than wolf density alone, yet without the potential spurious correlation problem of predation rate.

We estimated kill-rates for the Spray, Bow Valley, Cascade, and Fairholme wolf packs between 1986 and 2000 (chapter 3), excluding 1992/93 when intensive monitoring lapsed. We obtained kill-rate data for the Castle pack for one year only (1990/91), yet this pack was active from 1986/87 to 1991/92 in the western zone. Failing to include their kill-rates biases western zone kill-rate low during the period this pack was active. Therefore, we assumed kill-rates for the Castle pack were constant over this period and added the kill-rate estimate for 1990/91 (0.09 elk/day/pack, chapter 3) to Spray pack kill-rates in the western zone for all years between 1986/87 to 1991/92 for analyses.

Statistical Analyses

We tested how elk density, snow depth, wolf kill-rate, and human-caused mortality affected elk population growth from time t to t+1 over the 15-year time series (Fig. 3). We developed an a-priori set of candidate generalized linear models (GLMs) from these mortality factors (Appendix A4.1) that explicitly stated different hypotheses of factors affecting elk population growth rate as models (e.g., appendix C in Orians et al. 1997). We restricted models to first order terms, plus the interactions between snow and wolf predation and snow and elk density because of the limited length of the time series (n=15). GLM's were of the general form

$$r_t = \ln\left(\frac{N_{t+1}}{N_t}\right) = \beta_0 + \beta_1 X_1(t) + \beta_2 X_2(t) + \ldots . + \beta_m X_m(t) + \varepsilon \qquad \text{(equation 1)}$$

where t = 1 through 15 years, r_t= exponential population growth rate, β_0 is a constant, $\beta_1 \ldots \beta_m$ were coefficients of independent variables $X_1 \ldots . X_m$, ε is random error with the $\Sigma(\varepsilon)=0$. Candidate models were selected to align with previous models of ungulate population dynamics.

We used maximum likelihood estimation (type III) in PROC GENMOD in SAS 8.0 (SAS Institute, 1998) to estimate GLM's for elk population growth rate, and to estimate parameter coefficients and likelihood profiles. Akaike Information Criteria (AIC) was calculated from the general formula for AIC = -2 (log likelihood) + 2K, where K = the number of parameters, using the AIC_c correction for small sample sizes from

Burnham and Anderson (1998). We then used ΔAIC_c to select the best approximating model(s) within a zone, using an approximate cutoff of $\Delta AIC_c=4$ to describe the top model set (Burnham and Anderson 1998, Anderson et al. 2000). We used the sum of Akaike weights (ω_i) for each variable to rank them by importance (Burnham and Anderson 1998: 141) when model selection uncertainty arose in the top model set.

Autocorrelation, Time-lags, and Detecting Density Dependence

Autocorrelation, time lags, and the problem of detecting density dependence can affect regression analyses of population dynamics (Royama 1992, Post and Stenseth 1998). We examined autocorrelation functions (ACF) and partial autocorrelation functions (PACF) to test for autocorrelation in independent variables (Royama 1992:112). To test for time-lags between variables and growth rate, we used cross correlation function (CCF) analysis to explore the relationships between model variables and population growth rate. Many of our candidate models included N_t as an independent variable. Testing for density dependence by regressing N_t against population growth rate ($r_t = \ln(N_{t+1}/N_t)$) may negatively bias coefficients, increasing type I error rates (Royama 1992, Elkington 2000). The relatively short (n=15) length of our time series rendered the utility of many of the techniques reviewed by Elkington (2000) to detect density dependence uncertain.

To address these statistical problems, we followed advice from Elkington (2000) and others (Sinclair 1989, Royama 1992, Estes 1996, Minta et al. 1999) that studies of predator-prey dynamics should take a multi-pronged and pseudo-experimental approach to minimize these problems. Because of the psuedo-experimental nature of our across zone comparison, we did not account for autocorrelation unless differences existed between zones in the degree of autocorrelation for a particular variable. Furthermore, we did not correct elk density parameter estimates in growth rate models because time-series length, and therefore bias, was equal between zones.

Model Validation

We decomposed GLM's for each zone into difference equations representing linear models of elk abundance (N_t) following Merrill and Boyce (1991) as a limited form of model validation (sensu Boyce 2000). We used observed values for individual variables (Table 2) in the models to compare model predictions to observed elk population size, using the starting value for N_t at t=1. We converted density back to abundance for management interpretation. Where elk abundance was included in the model, we used mean values (Table 2) for other factors to predict abundance under average conditions using starting N_t,. This is equivalent to rewriting GLM's (eq.1) as a form of the logistic growth equation (Merrill and Boyce 1991), where the GLM becomes

$$N_{t+1} = N(t)e^{(\beta_0 + \beta_i X_i(t) + \ldots \beta_m X_m(t))} \qquad \text{(equation 2)}$$

where N_t= elk population size at time t, t = 1 to 15, and β_i= the coefficient of independent variable X_i. To select among the top model set for validation, we correlated predicted N_t and observed N_t for each model in the top model set in each zone (similar to analysis of explained variation in logistic regression, Mittleböck and Schemper 1996). We present model validation results for the model in the top set with the highest Pearson's correlation coefficient.

Results

Elk declined in the eastern and western zone, while increasing in the central zone over the study period (Fig. 4) after starting at relatively similar densities in 1986 (Table 2). Elk density in all three zones were autocorrelated (eastern zone ACF r=0.57, p=0.04, central r=0.45, p=0.02, west r= 0.68, p=0.06) to density at 1-time lag. However, because the degree and strength of autocorrelation were relatively similar between zones, we ignored effects on parameter estimates for our comparative approach across zones.

Mean snow depth varied throughout the period (range 30 to 80 cm, CV=32%, Table 2), yet we found no evidence for cumulative effects of snow of up to three years on population growth rate of elk (Appendix C). In addition, CCF analysis did not reveal any significant correlation's in time lags other than the current year between elk growth rate and snow depth. Therefore, we used snow depth at a lag of 1 (i.e., snow depth at time t) to determine effects on growth rate at time t.

Wolf kill-rates were highest in the western zone (0.17 kill/day/pack = k/d/p), intermediate in the eastern zone (0.12 k/d/p) when years when wolves were absent were excluded, and lowest in the central zone (0.06 k/d/p, Table 2, chapter 3). Wolf kill-rate varied considerably within zones (CV's from 67 to 82% , Table 2), but were the least variable in the western zone where wolves resided continuously through the study.

Human-caused mortality differed between zones (ANOVA, p=0.07, $F_{2,42}$=3.24), and was highest in the western zone (0.07 elk/day), followed by the eastern zone (0.06 elk/day), and central zone (0.05 elk/day). Western zone human-caused mortality was higher than the central zone (p=0.002), but not the eastern zone (p=0.14), and eastern and central human kill-rates did not differ (p=0.30, post-hoc bonferoni multiple comparisons).

We found no autocorrelation among zone-specific wolf or human kill-rates nor time-lag effects on population growth rate in any zones. Finally, model selection or parameter estimates were not different using either Castle pack corrected or uncorrected western zone kill-rates for the period that the Castle pack was active, supporting use of the Castle adjusted kill-rates in western zone analyses.

Eastern Zone – Medium Wolf Density

Several models should be considered as good models of population growth rate for the eastern zone (Table 3). The top model (SNOW) was only one and a half times as likely as the second model (WOLF + SNOW) to be the best approximating model, given the data (Table 3, the ratio of $\omega_{SNOW}/\ \omega_{SNOW+WOLF}= 1.5$ equals the likelihood of model 1 being the better approximating model, Burnham and Anderson, 1998: 126). Summing the Akaike weights ($\Sigma\omega_i$) for the four parameters included in the top model set (0-4 ΔAIC_c) ranked variables in the following order, SNOW (ω_i= 0.87), WOLF ($\Sigma\omega_i$= 0.37), WOLF*SNOW ($\Sigma\omega_i$= 0.12), and elk ($\Sigma\omega_i$= 0.11). Snow depth had a strong negative effect on elk population growth rate, as did predation by wolves (Table 3). Although the models SNOW + SNOW* WOLF, and SNOW + ELK were included in the top models set, parameter estimates for elk density and the snow-predation interaction had 95% likelihood ratio confidence intervals that broadly overlapped zero (Table 3).

Post-hoc exploratory analyses indicated a significant effect of the presence of wolves (0-no wolves, 1- wolves) on elk population growth rate. Following this presence/absence analysis, we divided the eastern zone into two separate time series, one with and one without wolves. Despite small sample sizes (n=8 years without wolves, n=7 with wolves), in simple univariate analyses elk density was negatively correlated with growth rate without wolf predation (Pearson's r=-0.77, P=0.03) but not with wolf predation (r=0.37, P=0.42). Wolf predation was negatively related to growth rate after 1992 when they recolonized this zone (r=-0.74, P=0.05). Snow depth was negatively related to elk growth rates with wolves present (r=-0.78, P=0.04) but not without wolves (r=-0.41, P=0.14). Finally, human-caused mortality was unrelated to growth rate with (P=0.19) or without wolf predation (p=0.39).

Central Zone – Low Wolf Density

The top model, ELK + TCH (ω_i=0.41) was 3 times more likely to be the best approximating model compared to the second model, ELK+ HUMAN+ TCH (ω_i=0.13, ΔAIC_c=2.4, Table 3). In the top model, elk density was strongly negatively related to population growth rate, and TCH fencing was positively related to growth rate (Table 3). Across all 4 top models, the effects of elk density were strongly negative (Table 3). Similarly, the effects of TCH fencing were strongly positive in the top model set (Table 3). The ELK*SNOW interaction term was not in any of the top models (Y=ELK* SNOW + ELK + TCH, ranked 9th, ΔAIC_c=4.9), and did not differ from 0 ($\beta_{ELK*SNOW}$= -4.0x10^5, S.E.= 2.0x10^4). The negative sign of snow depth and human coefficients in the second and fourth models were consistent with expectations (Table 3), but poor estimates indicated high variation.

Western Zone – High Wolf Density

Elk population growth in the western zone was best described by a constant rate of decline (Y=INTERCEPT, Table 3). Model selection was uncertain (low ω_i's for all models), and all models fit poorly (Table 3) . SNOW was the best predictor ($\Sigma\omega_i$= 0.28), followed by ELK($\Sigma\omega_i$ = 0.17), and HUMAN ($\Sigma\omega_i$= 0.07), but all variables had low akaike weights. Snow depth had a consistent and precisely estimated negative effect (Table 3). However, the negative effects of elk density and human mortality on growth rate were weak (Table 3).

Model Validation

In the eastern zone, the model WOLF+SNOW matched observed elk population trends closer than other models in the top set (Fig. 5a, observed N_t vs model-predicted N_t Pearsons r=0.88, P=0.03). In the central zone, the model ELK+HUMAN+ TCH matched observed elk populations closer (Fig. 5b, r=0.84, P=0.05) than other models. Using this central zone model under average human caused mortality with the TCH fenced, the elk population stabilized close to a carrying capacity, k, of 450 elk (Fig. 5b). In the western zone, the INTERCEPT and SNOW model matched observed population size similarly (r=0.92, P=0.04, r=0.91, P=0.04, Fig. 5b).

Discussion

The limiting effect of wolf predation and winter severity on elk population growth rate, and the regulatory effect of elk density on population growth rates without wolves in BNP, agrees with the findings of researchers studying northern ungulates elsewhere

(Skogland 1991, Messier 1994, Sæther 1997, Orians et al. 1997, Gaillard et al. 1998). Without predation by wolves, elk in the central zone increased during the early part of the study while elk in other zones decreased, evidence for the limiting role of wolf predation (Fig. 4). Reduction in human-caused mortality when the TCH was fenced in 1991 increased population growth rates for central zone elk. Population growth rate declined as density increased in the central zone, and was regulated around a carrying capacity (K) of approximately 10 elk/km^2 (~ 450 elk, Fig. 5b).

Snow depth and predation by wolves limited elk population growth in the eastern zone. When wolves recolonized this zone, the combination of predation by wolves and snow depth limited elk population growth rate and population density. In addition to support from the time-series models in the eastern zone, the simple univariate analyses confirmed these results in this zone. During the 7 years with predation by wolves, wolf predation and snow depth limited elk population growth rate. However, similar to the central zone, during the 8 years before wolf recolonization, elk density regulated population growth rate, and therefore elk population size to around 3.0 elk/km^2, or 200 elk (solving for 0 growth rate using the regression model, Elk population growth =1.10-0.35*ELKDEN, p=0.026, r^2=0.59).

The western zone (high wolf density) was more difficult to interpret. A constant rate of decline and no relationship between western zone kill-rate and elk growth rate seemed counter to results from the eastern zone. We feel this may be due to the pitfalls of correlative studies in predator-prey research (Royama 1996, Boyce and Anderson 1999). Boyce and Anderson (1999) described a three trophic level wolf-elk-vegetation population model, and explored the effects of where variation entered the model (wolf predation or vegetation biomass) on how much variation in elk numbers was explained by wolf predation or vegetation biomass. By alternately introducing random variation to wolf predation or vegetation biomass, they showed the degree of variation in either trophic level controlled how much elk numbers correlated with that trophic level. This demonstrated the difficulty obtaining insights into population dynamics through regression analyses, and suggested the lack of variation in elk population growth rates (Fig. 5c) rendered results from this zone uninformative. These results echo the caution of others (Royama 1996, Boyce and Anderson 1999, Minta et al. 1999) that key-factor type regression analyses on population growth rate have limited utility without an experimental approach.

Pseudo-experimental comparison of the eastern and central zones provided a clearer test for the limiting role of wolf predation, and approximated a before-after-control impact design (BACI, sensu Minta et al. 1999). Wolves remained absent in the central zone (control) throughout the study, while in the eastern zone (treatment) wolves recolonized (impact) mid-way. Support for the limiting effect of wolf predation comes from the comparison across zones for density-dependence and the effects of snow. With wolves present, density-dependence was not observed, although all three zones started at similar density ranges (Table 2), and a density dependent effect existed in the eastern zone before wolf recolonization. Therefore, the presence of wolves seems to limit elk below densities which would regulate growth rates, similar to other northern ungulates (Gasaway, 1992, Jedrzrejewska et al. 1997).

Winter severity (snow depth) negatively affected population growth rates with wolves in the eastern zone. However, contrary to our predictions and previous research showing the interactive effects of density and weather on population growth rates in ungulate populations without wolves (Picton 1984, Portier et al. 1998, Milner et al. 1999), the effects of snow did not manifest without predation in the central zone. The lack of a SNOW or SNOW*ELK interaction effect in the central zone could arise because starving elk follow a risk-sensitive foraging strategy (Sinclair and Arcese 1995), leaving the relatively safe central zone to forage on more abundant vegetation elsewhere in deep snow winters. Density-dependent starvation mortality of elk in BNP during winter is extremely rare (Parks Canada, unpubl.data), and wolf predation is known to be at least partially compensatory (e.g, Mech et al. 1995). Therefore, at high elk density in BNP in the central zone, the effects of snow do not manifest, perhaps because on a regional scale predation by wolves is partially compensatory on starving elk. This pattern may characterize the landscape scale of wolf predation on ungulate populations, and help explain the continental pattern of high winter kill in ungulate populations without wolf predation (Leopold et al. 1947).

The lack of a strong SNOW*WOLF interaction in the eastern zone may be an artifact of the temporal scale of the time series analysis. During deep snow winters, wolves ate less of each kill (M.Hebblewhite, unpubl.data), and Huggard (1993a) found kill-rates increased with increasing snow depths, revealing the importance of the interaction of snow depth and predation within a particular winter. Using mean values of snow depth and predation for each winter in time series analyses masks this within year snow-predation interaction. Therefore, we believe the main effects of snow depth on elk are realized through this within winter interaction with wolf predation in BNP. The fact that there was no SNOW effect in the central zone also supports this interpretation.

Inferences from our study would have been strengthened if we had measures of calf and adult survival. Without such age-specific survival data, we were unable to infer how snow, wolf predation, or density affect demographic processes. Features of our study area should be considered before our findings are generalized to other wolf-ungulate systems. Despite the strong evidence for elk sub-population structure (Woods 1991, Paquet et al. 1996, Woods et al. 1996, McKenzie 2001) and differences in wolf predation in BNP that align with the analysis zones (chapter 3, Fig. 1, 2), such boundaries are arbitrary at some level. We assume decreased elk numbers in the eastern zone to be the result of direct lethal effects of predation. Following wolf recolonization of the eastern zone, elk may have adopted a strategy to minimize predation risk that included spending more time in the central (wolf-free) zone. If this occurred for even some elk in the eastern zone, our analysis includes both the direct lethal effects of predation and the indirect effects. Regardless, the consequences of direct and indirect effects could manifest similarly on other trophic levels (Schmitz 1998).

In the analysis of complex ecological systems such as ungulate population dynamics, using an information-theoretic approach to guide data-based model selection and inference offers several advantages. Considering alternate models, especially with high model selection uncertainty, allowed us to gain a deeper understanding of factors affecting elk population dynamics. Adopting a single model for inference (i.e., using stepwise model selection) may have led us to overlook the important effects of wolf predation and snow depth in the across zone comparison, and the significance of the univariate before and after comparison in the eastern zone. Model selection uncertainty is not a weakness of this approach, as such uncertainty is a realistic measure of our confidence in the models, given the data (Burnham and Anderson, 1998).

We used this approach (Appendix C.3) to examine the longstanding debate surrounding analysis of factors affecting moose population dynamics on Isle Royale (Mech et al. 1987, Messier 1991, McRoberts et al. 1995, Messier 1995a, Post and Stenseth 1998). We simultaneously compared 11 competing models explaining moose population growth rate using AIC, and found the best model aligned with Messier's (1991) moose and wolf density model, which was 4 times as likely as any other model, and 60 times as likely as Mech et al.'s (1987) original snow (1 year or 3 year lag) model (Appendix C3). Adopting the multiple working hypotheses approach would have pre-empted debate surrounding these data, and future analyses of factors affecting ungulate population dynamics should adopt an information-theoretic approach.

Wolf predation on elk in the eastern zone had positive conservation implications for ecosystem processes within Parks Canada's mandate to maintain ecological integrity (Government of Canada 1988). Declining elk density as a result of predation by wolves reduced elk herbivory on riparian willow (*Salix* spp.) and trembling aspen (*Populus tremuloides*, Nietvelt 2000, White 2001), and reduced indirect and exploitative competition of elk with moose (Hurd 1999), beaver (*Castor canadensis*), and riparian passerines (Nietvelt 2000). Although a quantitative test of whether wolves are acting as a keystone species (Menge et al., 1994, Power et al. 1996) has not been conducted, this indirect evidence suggests a causal mechanism of human disturbance altering wolf distribution, with associated cascading effects to lower trophic levels. Future research should test this hypothesis.

Gaillard et al. (1998) suggested constant adult survival and variable juvenile recruitment characterized northern ungulate population dynamics. Their review included populations with and without major predators such as wolves in sensitivity analyses of ungulate population growth rate. Although we report population growth rates and not age-specific survival of elk in BNP, we show ungulate population processes differ with and without wolves, and wolf predation appears to reduce interaction of density on ungulate population dynamics. Therefore, with wolf predation, we may expect juvenile and/or adult survival to vary less with environmental factors, which could dramatically alter results of sensitivity analyses. Northern ungulates evolved with predators such as wolves, and combining results from studies with and without predation may have serious implications for meta-analyses (sensu Gaillard et al. 1998) of ungulate population dynamics.

Conclusions

Predation by wolves and snow depth limited elk growth rates in BNP, and density regulated elk population growth without predation by wolves. Wolf predation in BNP appears capable of reducing elk densities below the range at which density-dependent processes occur. We found no evidence of interactive effects of snow depth and density as described in ungulate populations without predators. Humans can have dramatic effects on ungulate population dynamics by altering the distribution of predators, and these effects may ripple down through trophic cascades to herbivores and vegetation. Our analysis offers an example of the benefits of adopting an information-theoretic approach to data-based model selection and inference in complex biological systems. Within the context of protected area management and conservation across North American landscapes, restoration of wolves has the potential to restore many of these ecosystems through their effects on elk population dynamics, and ecologists should take advantage of pseudo-experimental conditions that wolf restoration will present.

Table 1. Summary of wolf density, predation, and elk mortality patterns in the different zones of the Bow Valley of Banff National Park (from Green et al. 1996, Paquet et al. 1996, Woods et al. 1996).

Zone	Wolf Density	Wolf Predation	Human Mortality
Eastern	Medium[1]	Partial[1]	Low highway, high railway
Central	Low	Almost None	Low highway after 1990, and low railway
Western	High	Full	High highway, high railway

1 – Wolves recolonized this zone mid-way through the study, and then only used areas north of the Trans Canada Highway.

Table 2. Bow Valley elk population data from Banff National Park, Alberta, from 1986 to 2000. See text for variable descriptions. Mean and coefficient of variation are presented. Mean height of snowpack were the same for all three zones.

a) Central Zone

Bioyear	Elk N_t	r_t	Elk/km^2	Snow (cm)	Human (Elk/day)	Wolf (Elk/d/w)
1985/86	223	0.40	5.20	39.00	0.12	-----
1986/87	334	-0.19	7.79	45.51	0.07	0.13
1987/88	277	0.29	6.46	30.18	0.01	0.02
1988/89	369	0.04	8.60	45.83	0.01	0.10
1989/90	385	-0.04	8.97	39.54	0.03	0.04
1990/91	371	0.10	8.65	80.39	0.09	0.11
1991/92	412	-0.05	9.60	32.64	0.01	0.01
1992/93	390	0.31	9.09	32.89	0.01	-----
1993/94	533	-0.15	12.42	46.84	0.01	0.07
1994/95	459	0.08	10.70	45.79	0.06	0.02
1995/96	497	-0.08	11.59	62.92	0.04	0.01
1996/97	458	-0.01	10.68	67.24	0.08	0.10
1997/98	455	-0.16	10.61	30.96	0.07	0.10
1998/99	388	0.19	9.04	46.08	0.06	0.02
1999/00	467	0.00	10.89	33.28	0.04	0.21
2000/01	467[1]	N/A	----	----	----	----
Mean	401.20	0.05	9.35	45.27	0.05	0.07
CV	-----	----	20.50	32.29	73.77	82.40

1 –This count includes the 153 elk translocated during the preceding winter.

2b) Eastern and Western Zone

	Eastern Zone					Western Zone				
Bioyear	Elk N_t	r_t	Elk/ km^2	Human (Elk/day)	Wolf (Elk/ d/w)	Elk N_t	r_t	Elk/ km^2	Human (Elk/day)	Wolf (Elk/ d/w)
1985/86	139	0.53	2.08	0.06	0.00	411	-0.21	2.20	0.149	**----**
1986/87	237	-0.22	3.55	0.08	0.00	332	0.10	1.78	0.199	0.47[1]
1987/88	191	0.37	2.86	0.06	0.00	366	-0.24	1.96	0.061	0.41[1]
1988/89	277	-0.21	4.15	0.06	0.00	288	-0.28	1.54	0.094	0.19[1]
1989/90	225	-0.06	3.37	0.06	0.00	218	0.33	1.17	0.099	0.34[1]
1990/91	211	-0.40	3.16	0.09	0.00	302	-0.52	1.62	0.238	0.28[1]
1991/92	141	0.27	2.11	0.10	0.00	179	-0.46	0.96	0.061	0.28[1]
1992/93	184	0.04	2.75	0.07	0.00	113	-0.25	0.61	0.028	----
1993/94	192	0.01	2.87	0.05	0.16	88	-0.20	0.47	0.066	0.27
1994/95	194	-0.11	2.90	0.04	0.12	72	0.32	0.39	0.017	0.08
1995/96	174	-0.66	2.60	0.10	0.28	99	-0.70	0.53	0.055	0.13
1996/97	90	-0.22	1.35	0.03	0.25	49	-0.20	0.26	0.022	0.04
1997/98	72	0.27	1.08	0.07	0.03	40	0.22	0.21	0.039	0.03
1998/99	94	-0.28	1.41	0.03	0.07	50	0.32	0.27	0.061	0.16
1999/00	71	0.03	1.06	0.05	0.04	69	-0.01	0.37	0.039	0.04
2000/01	73	N/A	----	----	----	68	N/A	----	----	----
Mean	166.1	-0.04	2.49	0.06	0.12	178.4	-0.12	0.96	0.08	0.17
CV	37.9	----	37.90	34.57	82.9	72.80	-----	-----	79.87	67.2

1- These are Castle pack adjusted western zone kill-rate

Table 3. Top GLM model set by Bow Valley zone for elk population growth rate, with model deviance, model structure and corresponding ΔAIC_c and Akaike weight (ω_i(Burnham and Anderson 1998). Maximum likelihood estimates (MLE, type III) for coefficients in the models are presented with standard errors, coefficients with likelihood ration chi-square probabilities <0.05 are highlighted in black, and <0.10 marked by an asterix. Coefficients are reported in the order in the model, i.e. for β_{i}, $_i$= 1 if the model only has one parameter.

Model Structure	Deviance	ΔAIC_c	ω_i	β_0	S.E.	β_i	S.E.	β_i	S.E.	β_i	S.E.
Eastern Zone Models											
1. $\beta_0+\beta_1$(SNOW)	0.609	0	0.37	**0.68**	0.175	**-0.016**	0.004	----		-----	
2. $\beta_0+\beta_1$(SNOW)+β_2(WOLF)	0.573	0.63	0.27	**0.63**	0.177	**-0.014**	0.004	**-0.62**	0.25	-----	
3. $\beta_0+\beta_1$(SNOW)+β_2(WOLF*SNOW)	0.577	2.38	0.12	**0.619**	0.183	**-0.014**	0.004	-0.009	0.010	-----	
4. $\beta_0+\beta_1$(SNOW)+β_4(ELK)	0.586	2.60	0.11	**0.767**	0.206	**-0.016**	0.004	-0.044	0.05	-----	
Central Zone Models											
1.$\beta_0+\beta_4$(ELK)+β_5(TCH)	0.175	0	0.41	**0.89**	0.174	**-0.106**	0.023	**0.23**	0.09	**-----**	
2.$\beta_0+\beta_3$(HUMAN)+β_4(ELK)+β_5(TCH)	0.157	2.40	0.13	**1.03**	0.19	-1.14	0.87	**0.118**	0.02	**0.267**	0.09
3.$\beta_0+\beta_4$(ELK)	0.255	2.44	0.12	**0.632**	0.173	**-0.062**	0.018			**-----**	
4.$\beta_0+\beta_1$(SNOW)+β_4(ELK)+β_5(TCH)	0.172	3.60	0.07	0.924	0.19	-0.001	0.02	**-0.106**	0.02	0.238	0.09
Western Zone Models											
1.$\beta_0+\varepsilon$	1.459	0	0.21	**-0.120**	0.081	----		----		-----	
2.$\beta_0+\beta_1$(SNOW)	1.229	0.11	0.20	0.278	0.25	-0.01*	0.005	----		-----	
3.$\beta_0+\beta_4$(ELK)	1.364	1.68	0.09	-0.007	0.135	-0.12	0.116	----		----	
4.$\beta_0+\beta_1$(SNOW)+β_4(ELK)	1.127	2.00	0.08	0.40	0.026	-0.01*	0.005	0.12	0.105	-----	
5.$\beta_0+\beta_3$(HUMAN)	1.406	2.13	0.07	-0.043	0.13	-0.95	1.25	----			

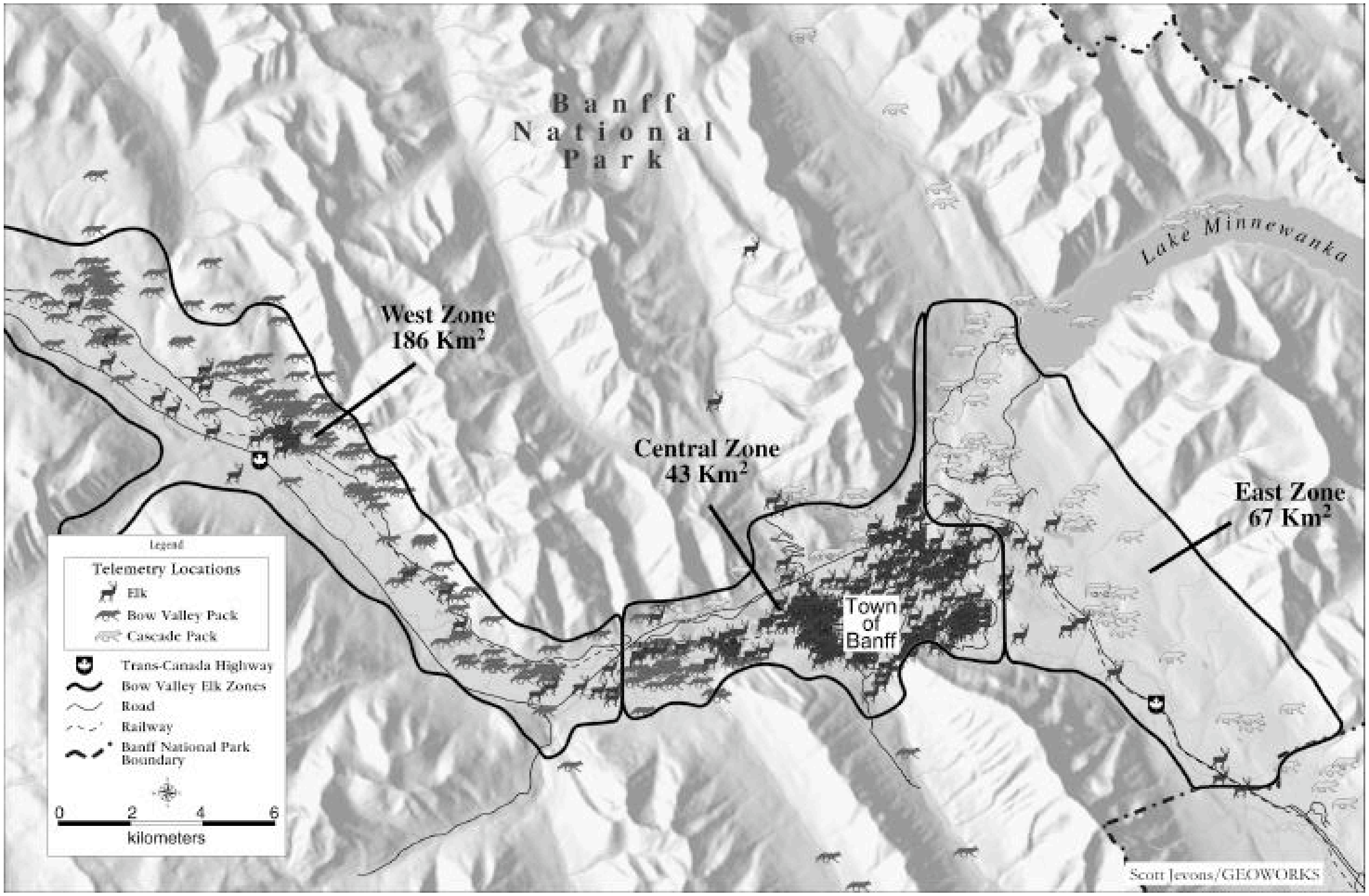


Figure 1. Wolf and elk distribution during the winters in the Bow Valley of BNP, Alberta, 1997 to 1999, using random radio-telemetry locations (n=363) for radio-collared wolves in the Cascade and Bow Valley pack, and 45 radio-collared elk (J.McKenzie, unpubl.data). Bow Valley zones used in analyses were derived from aerial survey units (see Fig. 2), and correspond with high (western), medium (eastern) and low (central) wolf density and predation.

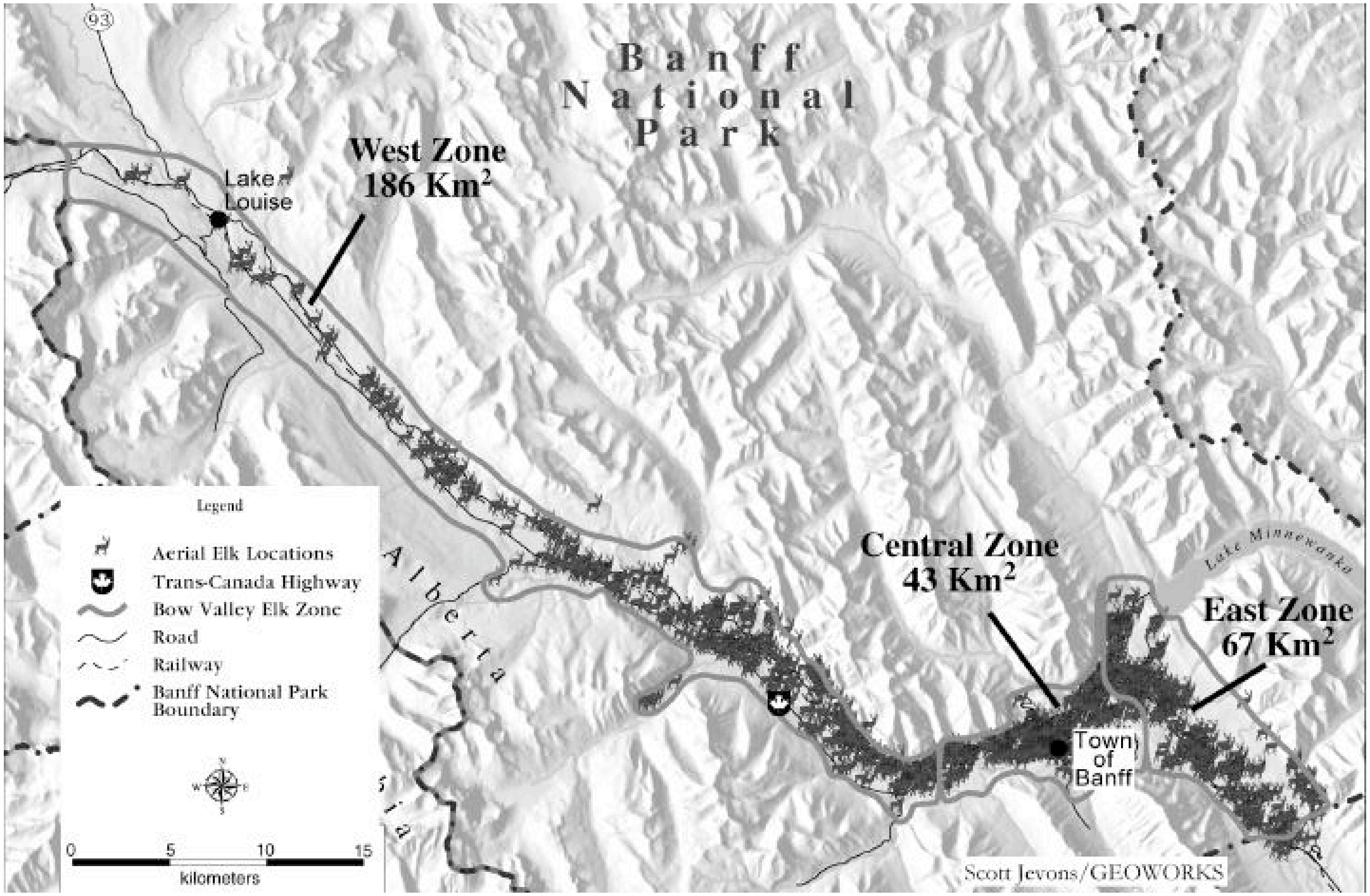


Figure 2. Distribution of elk observed on annual midwinter aerial elk surveys in the Bow Valley of Banff National Park, Alberta, from 1986 to 2000. The elevation of all elk sightings collected on annual surveys were used to determine the elevation below which 99% of all elk locations were found to delineate the boundaries of the Bow Valley zones used for zone-specific analyses (east, central, and western zones).

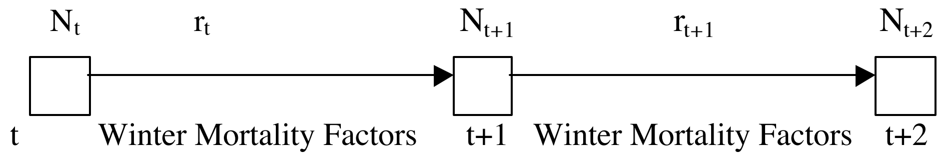


Figure 3. Annual life cycle of elk in BNP used for analysis showing late April survey periods in the squares, and intervals where growth and mortality occur as arrow lines.

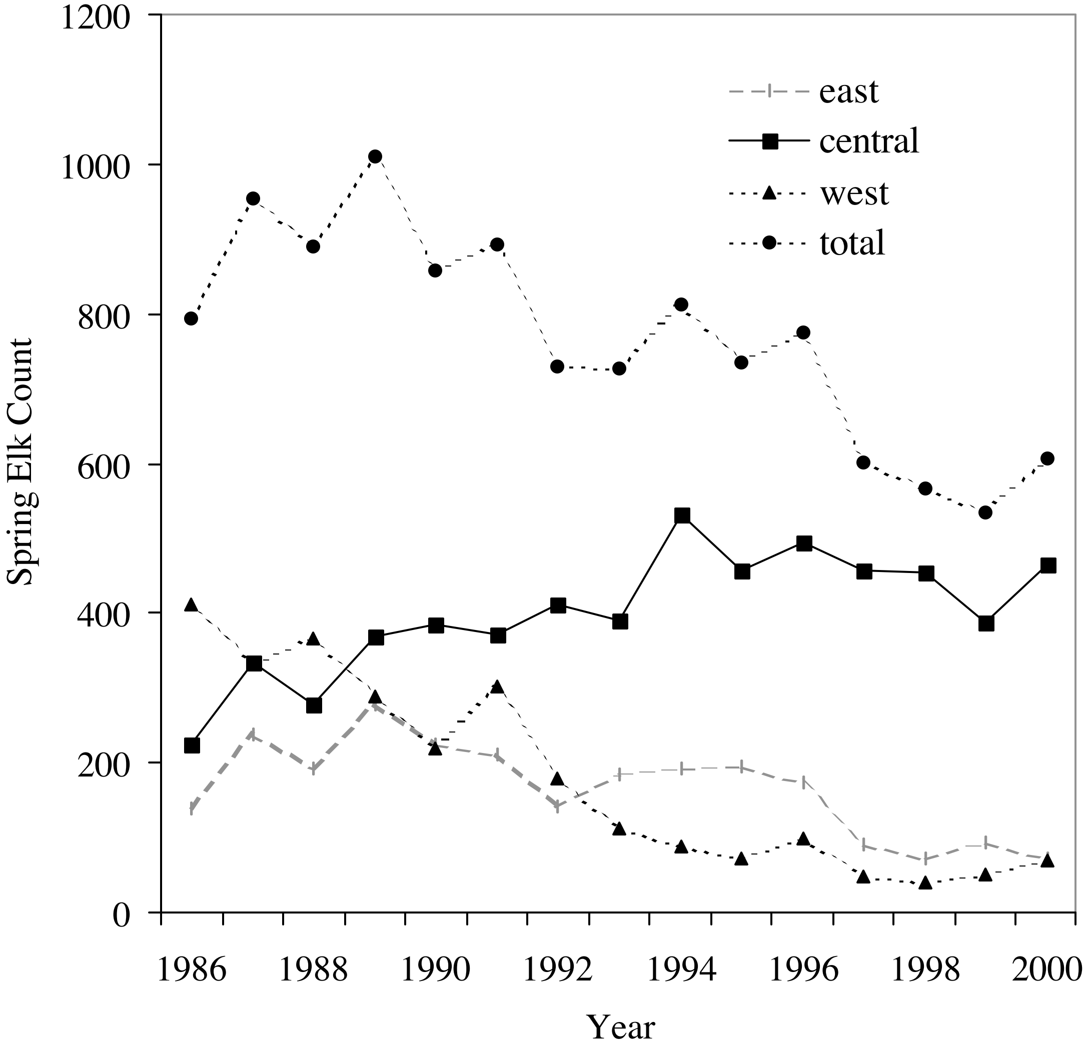
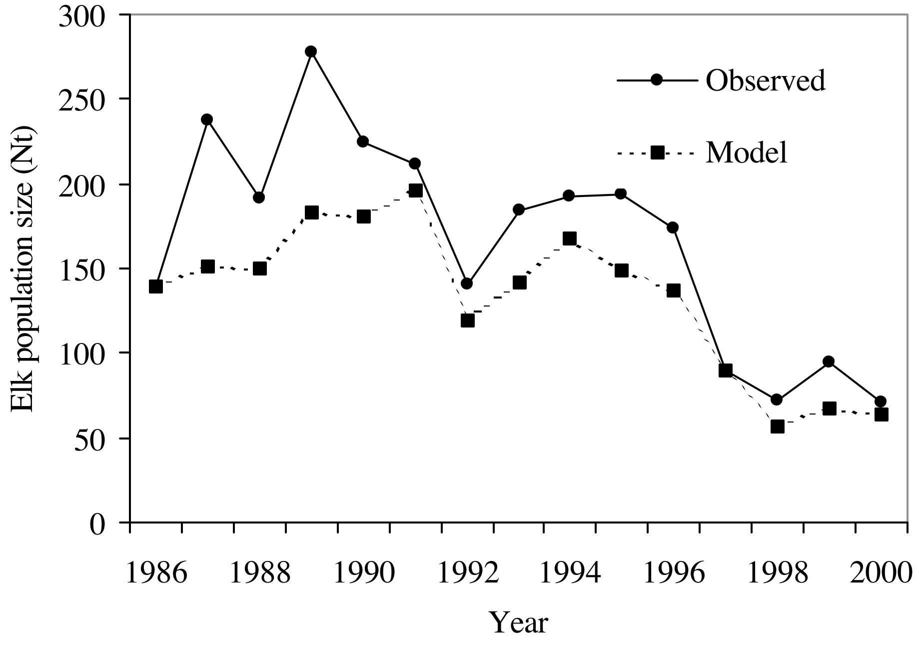
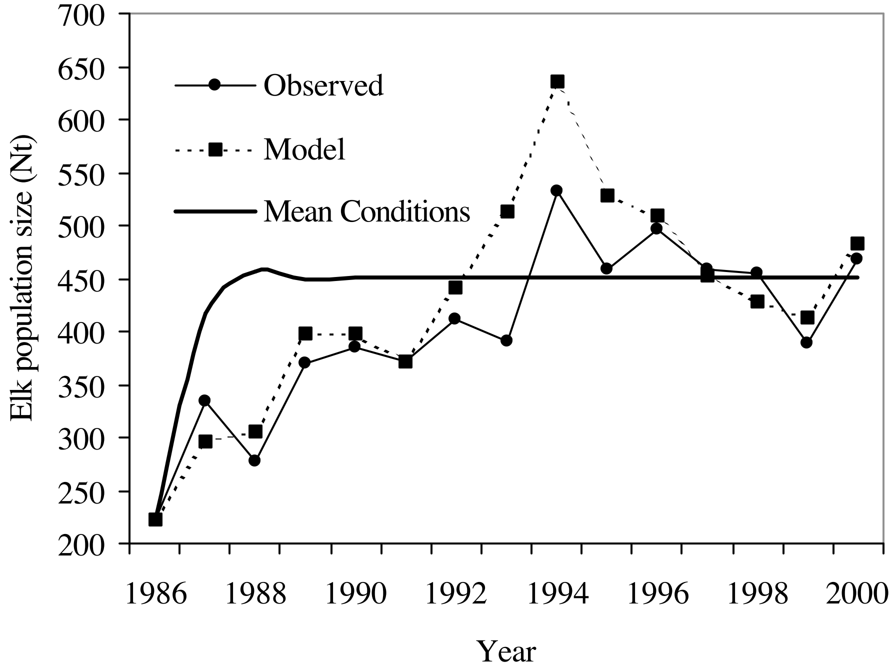


Figure 4. Elk population trends in the three zones (east, central, west) and total in the Bow Valley of Banff National Park, Alberta, from aerial elk surveys during late winter, 1986 to 2000.

a) Eastern Zone (medium wolf density), Y= SNOW+WOLF



b) Central zone (low wolf density) Y=ELK+HUMAN+TCH



c) Western zone (high wolf density) Intercept Model and Y=SNOW

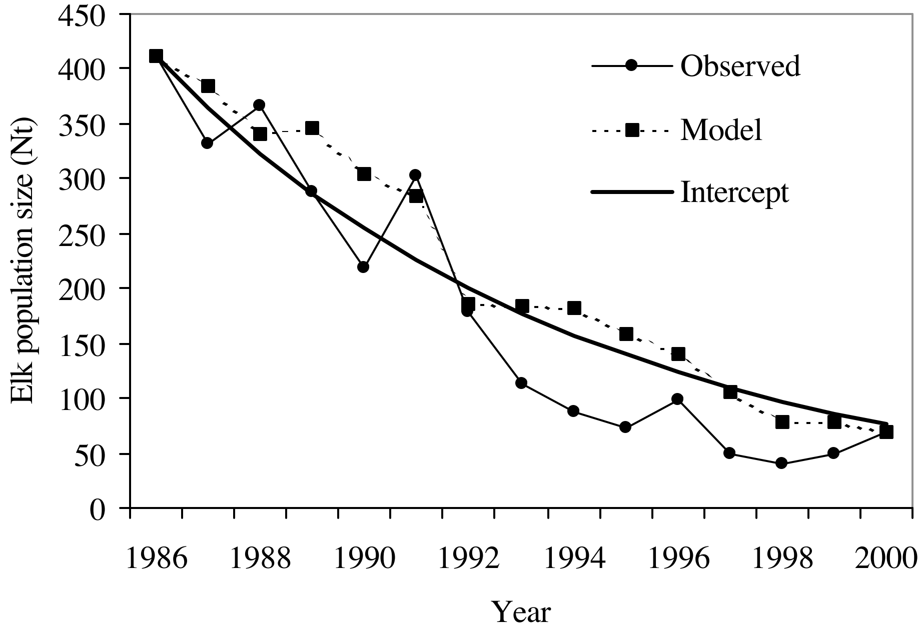


Figure 5. Observed spring elk counts in Banff National Park (BNP) zone versus elk count predicted using top candidate generalized linear models converted to difference equations for each zone from 1985 to 2000. For the central zone, elk population size is predicted assuming average human caused mortality and a fenced highway using the GLM expanded as an approximation of the logistic growth equation.

Appendix C.1 Candidate Models for GLM Analysis

Table A4.1. Candidate models for determining factors that affect elk population dynamics, where the dependent variable in all models is elk population growth rate, and independent variables are listed in Table 2. In the eastern and western zones, a total of 32 (without TCH) models are in the candidate set, in the central zone there is a total of 58 models. β_0=intercept, β_1=Snow Depth, β_2= Wolf Predation, β_3=Human-caused mortality, β_4= elk density β_5= TCH fenced, β_6= Interaction term.

Candidate Model Description	Model Structure
GLOBAL MODEL	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_3X_3+\beta_4X_4+\beta_5X_5+\beta_6X_6+\varepsilon$
INTERCEPT ONLY	$Y=\beta_0+\varepsilon$
WOLF	$Y=\beta_0+\beta_2X_2+\varepsilon$
SNOW	$Y=\beta_0+\beta_1X_1+\varepsilon$
ELK	$Y=\beta_0+\beta_4X_4+\varepsilon$
HUMAN	$Y=\beta_0+\beta_3X_3+\varepsilon$
TCH [a]	$Y=\beta_0+\beta_5X_5+\varepsilon$
INTERACTION[b]	$Y=\beta_0+\beta_6X_6+\varepsilon$
WOLF + SNOW	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\varepsilon$
WOLF + ELK	$Y=\beta_0+\beta_2X_2+\beta_4X_4+\varepsilon$
WOLF + HUMAN	$Y=\beta_0+\beta_2X_2+\beta_3X_3+\varepsilon$
WOLF + TCH[a]	$Y=\beta_0+\beta_2X_2+\beta_5X_5+\varepsilon$
WOLF + INTERACTION[b]	$Y=\beta_0+\beta_2X_2+\beta_6X_6+\varepsilon$
TCH[a] + INTERACTION[b]	$Y=\beta_0+\beta_5X_5+\beta_6X_6+\varepsilon$
SNOW + ELK	$Y=\beta_0+\beta_1X_1+\beta_4X_4+\varepsilon$
SNOW + HUMAN	$Y=\beta_0+\beta_1X_1+\beta_3X_3+\varepsilon$
SNOW + TCH[a]	$Y=\beta_0+\beta_1X_1+\beta_5X_5+\varepsilon$
SNOW + INTERACTION	$Y=\beta_0+\beta_1X_1+\beta_6X_6+\varepsilon$
ELK + HUMAN	$Y=\beta_0+\beta_4X_4+\beta_3X_3+\varepsilon$
ELK + INTERACTION	$Y=\beta_0+\beta_4X_4+\beta_6X_6+\varepsilon$
ELK + TCH[a]	$Y=\beta_0+\beta_4X_4+\beta_5X_5+\varepsilon$
HUMAN + INTERACTION	$Y=\beta_0+\beta_3X_3+\beta_6X_6+\varepsilon$
HUMAN + TCH[a]	$Y=\beta_0+\beta_3X_3+\beta_5X_5+\varepsilon$
WOLF + ELK + SNOW	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_4X_4+\varepsilon$
WOLF + ELK + HUMAN	$Y=\beta_0+\beta_2X_2+\beta_3X_3+\beta_4X_4+\varepsilon$
WOLF + ELK + TCH[a]	$Y=\beta_0+\beta_2X_2+\beta_4X_4+\beta_5X_5+\varepsilon$
WOLF + ELK + INTERACTION[b]	$Y=\beta_0+\beta_2X_2+\beta_4X_4+\beta_6X_6+\varepsilon$
WOLF + HUMAN + SNOW	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_3X_3+\varepsilon$
WOLF + HUMAN + TCH[a]	$Y=\beta_0+\beta_2X_2+\beta_3X_3+\beta_5X_5+\varepsilon$
WOLF + HUMAN + INTERACTION[b]	$Y=\beta_0+\beta_2X_2+\beta_3X_3+\beta_6X_6+\varepsilon$
WOLF + SNOW + TCH[a]	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_5X_5+\varepsilon$
WOLF + SNOW + INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_6X_6+\varepsilon$
SNOW + ELK + HUMAN	$Y=\beta_0+\beta_1X_1+\beta_3X_3+\beta_4X_4+\varepsilon$
SNOW + ELK + INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_3X_3+\beta_6X_6+\varepsilon$
SNOW + HUMAN + TCH[a]	$Y=\beta_0+\beta_1X_1+\beta_3X_3+\beta_5X_5+\varepsilon$
SNOW + HUMAN + INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_3X_3+\beta_6X_6+\varepsilon$

ELK + HUMAN + TCH[a]	$Y=\beta_0+\beta_3X_3+\beta_4X_4+\beta_5X_5+\varepsilon$
ELK + HUMAN + INTERACTION[b]	$Y=\beta_0+\beta_3X_3+\beta_4X_4+\beta_6X_6+\varepsilon$
ELK + SNOW + TCH[a]	$Y=\beta_0+\beta_1X_1+\beta_4X_4+\beta_5X_5+\varepsilon$
ELK + SNOW + INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_4X_4+\beta_6X_6+\varepsilon$
WOLF + TCH[a] + INTERACTION[b]	$Y=\beta_0+\beta_2X_2+\beta_5X_5+\beta_6X_6+\varepsilon$
ELK + TCH + INTERACTION	$Y=\beta_0+\beta_3X_3+\beta_5X_5+\beta_6X_6+\varepsilon$
HUMAN + TCH+ INTERACTION	$Y=\beta_0+\beta_4X_4+\beta_5X_5+\beta_6X_6+\varepsilon$
SNOW + TCH + INTERACTION	$Y=\beta_0+\beta_2X_2+\beta_5X_5+\beta_6X_6+\varepsilon$
ELK + SNOW + HUMAN + TCH[a]	$Y=\beta_0+\beta_1X_1+\beta_3X_3+\beta_4X_4+\beta_5X_5+\varepsilon$
ELK + SNOW + HUMAN + INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_3X_3+\beta_4X_4+\beta_6X_6+\varepsilon$
WOLF + SNOW + ELK + HUMAN	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_3X_3+\beta_4X_4+\varepsilon$
WOLF + SNOW + ELK + INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_3X_3+\beta_6X_6+\varepsilon$
WOLF + HUMAN + ELK + TCH[a]	$Y=\beta_0+\beta_2X_2+\beta_3X_3+\beta_4X_4+\beta_5X_5+\varepsilon$
WOLF + HUMAN + ELK + INTERACTION[b]	$Y=\beta_0+\beta_2X_2+\beta_3X_3+\beta_4X_4+\beta_6X_6+\varepsilon$
WOLF + ELK + SNOW + TCH[a]	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_4X_4+\beta_5X_5+\varepsilon$
WOLF + SNOW +TCH[a] +INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_5X_5+\beta_6X_6+\varepsilon$
WOLF + ELK + TCH[a] +INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_4X_4+\beta_5X_5+\beta_6X_6+\varepsilon$
WOLF + HUMAN + TCH[a] +INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_3X_3+\beta_5X_5+\beta_6X_6+\varepsilon$
SNOW + ELK + TCH[a] +INTERACTION[b]	$Y=\beta_0+\beta_2X_2+\beta_4X_4+\beta_5X_5+\beta_6X_6+\varepsilon$
SNOW + HUMAN + TCH[a] +INTERACTION[b]	$Y=\beta_0+\beta_2X_2+\beta_3X_3+\beta_5X_5+\beta_6X_6+\varepsilon$
ELK + HUMAN + TCH[a] +INTERACTION[b]	$Y=\beta_0+\beta_3X_3+\beta_4X_4+\beta_5X_5+\beta_6X_6+\varepsilon$
WOLF + ELK + SNOW + INTERACTION[b]	$Y=\beta_0+\beta_1X_1+\beta_2X_2+\beta_4X_4+\beta_5X_5+\varepsilon$

a. TCH models not run in the eastern and western zone.
b. The interaction term was SNOW*WOLF in the eastern and western zone, and SNOW*ELK in the central zone.

Appendix C.2. Cumulative snow analyses

Table C.2. Pearson's correlation (R) between cumulative measures of mean snowpack height over 1 to 3 previous winters on elk population growth rate in BNP. (P-values at $\alpha=0.05$ are presented.)

Cumulative		Bow Valley Zone		
Winters		Eastern	Central	Western
1	R =	-0.745	-0.398	-0.150
	P =	<0.001	0.142	0.595
2	R =	-0.333	-0.372	-0.360
	P =	0.225	0.172	0.188
3	R =	-0.422	-0.292	-0.216
	P =	0.117	0.292	0.436

Appendix C.3. Isle Royale Moose Population Dynamics Re-analysis Using an Information-Theoretic Approach to Model Selection

We re-analyzed the original (non-transformed) moose population data from Messier (1991) as a further example of the utility of the information theoretic approach. We simplified these data to the independent variables moose density, wolf density, current year snow depth and cumulative snow depth over the previous three years, and the dependent variable exponential growth rate. The competing models of Messier (1991) and Mech et al. (1987) can be generalized to Moose+Wolf, and Snow (1 or 3 year time lag). We generated an a-priori model set of all non-interaction models (not including models with 2 snow variables, for a total of 11 models, Table A4.2) that explained population growth rate (ln(lambda)), and used AIC_c to select the best candidate model given the data using methods described above for our analyses in BNP. The best approximating model was Y=Moose + Wolf, and this model had high Akaike weight (ω_i=0.68) and low model deviance (Table A4.2). Considering parameter estimates from the top 3 models (i.e., within 0-4 ΔAIC_c) strengthened inference about the important role of moose and wolf density on moose population growth on Isle Royale, and the low likelihood of any snow effect (Table A4.2). This simple analysis agrees with Messier (1991, 1995), but more importantly illustrates the utility of considering multiple working hypotheses simultaneously when compared to the acrimonious and confusing debate in the literature (Mech et al. 1987, Messier 1991, McRoberts et al. 1995, Messier 1995a, Post and Stenseth, 1998). Despite Post and Stenseth's (1998) sophisticated re-analysis using step-wise model selection, how alternate models would have fit these data is unknown.

Table C.3. Re-analysis of the original data from Messier (1991) from Isle Royale Moose-wolf population dynamics research, showing the candidate generalized linear model (GLM) set used, the top model, ΔAIC_c, Akaike weights (ω_i), and parameter coefficients with standard errors. The dependent variable in all GLM's was the natural logarithm of percent change (lambda) described in Messier (1991). Analysis was similar to methods described in detail for elk population in BNP. Coefficients with log likelihood chi-square probabilities <0.05 and the top model are indicated in bold.

Model Description	Deviance	ΔAIC_c	ω_i	β_0	S.E.	β_1	S.E.	β_2	S.E.	β_0	S.E.
Moose + Wolf	0.254	0.00	0.66	**1.05**	0.23	**-0.53**	0.12	**-0.06**	0.018	-----	
Moose + Wolf + Snow1	0.244	3.01	0.15	**1.05**	0.23	**-0.58**	0.14	**-0.07**	0.02	0.0002	0.0003
Moose + Wolf + Snow3	0.251	3.45	0.12	**1.13**	0.30	**-0.52**	0.012	**-0.06**	0.02	-0.009	0.02
Moose	0.440	5.73	0.04	0.41	0.19	-0.31	0.14	-----		-----	
Moose + Snow3	0.434	8.60	0.01	**0.52**	0.32	**-0.30**	0.14	0.012	0.026	-----	
Moose + Snow1	0.440	8.81	0.01	**0.41**	0.19	**-0.31**	0.15	0.00004	0.0004	-----	
Wolf	0.551	9.34	0.01	0.11	0.14	-0.02	0.02	-----		-----	
Snow1	0.553	9.38	0.01	0.12	0.15	-0.0004	0.0004	-----		-----	
Snow3	0.565	9.74	0.01	0.20	0.32	-0.02	0.03	-----		-----	
Wolf + Snow1	0.520	11.47	0.00	0.26	0.20	-0.02	0.02	-0.0004	0.0004	-----	
Wolf + Snow3	0.536	11.95	0.00	0.32	0.34	-0.02	0.02	-0.02	0.03	-----	

Chapter 5: Conclusions, Management Implications and Recommendations.

I summarize key management implications and recommendations from the separate chapters first, and then provide a synthesis and conclusions.

Chapter 2 – Effects of elk herding on wolf predation

Wildlife managers and researchers should focus attention on the relationships between elk population size, herd size, and the number of herds because of the importance of these relationships to understanding the population consequences of predation by wolves on elk. Behavior may differ in areas without wolves. These relationships may not be the same in increasing or decreasing elk populations, because elk behavior may affect relationships differently dependent on population trajectory.

The evolutionary ecology of elk herding suggests elk minimize predation risk from wolves by either living in small, difficult to find herds, or by living in large herds and minimizing risk through dilution. These strategies may align with seasonal migration strategies. Urban elk populations should be viewed in this evolutionary framework of avoiding predation risk, and the behavioral plasticity of elk may allow switching between strategies to seek out predation refugia. Therefore, managers may expect the development of urban elk populations in landscapes where wolves are recolonizing. Factors that may contribute to this include the provision of high-quality forage, such as on golf courses (e.g., surrounding Canmore, AB) and with winter feeding programs (i.e., Jackson, WY).

Chapter 3 – Estimating wolf killing rates in a multi-prey system

Humans can have a dramatic impact on wolf kill-rates. By excluding wolf use of areas through fragmentation or high human use, humans may affect wolf-prey relationships, leading to predation refugia for elk and other ungulates. This has broad ecosystem management implications where wolves, elk and humans are sympatric.

The correlation between elk and wolf density and wolf kill-rates, and the limiting effect of wolves on elk populations, suggests declines in wolf populations may be expected after wolf populations rapidly increase following recolonization. Pup production and survival increased with prey density elsewhere (e.g., Boertje and Stephenson 1992), suggesting wolf populations may be able to absorb higher levels of human caused mortality during early recolonization than after populations have been established for some time.

Chapter 4 – Factors Affecting Population Dynamics

Without wolf predation, carrying capacity (K) for elk is regulated by density around 450 elk (~10 elk/ km^2) in the central zone. Translocation as a management tool to reduce elk population density in this area is of limited long-term utility because removing elk without reducing K will result in increased population growth rate back to carrying capacity.

Wolf predation appears capable of limiting elk populations in conjunction with snow depth. Increasing predation rates of wolves to reduce elk in the central zone is consistent with Parks Canada's policies of minimal interference to maintain ecological integrity through ecological process management (Parks Canada 1994). Maintaining predation by wolves in the central zone requires restoring carnivore movements surrounding the Townsite through corridor restoration, and reducing human caused mortality of wolves in BNP. Other measures to reduce the carrying capacity for elk in the central zone include aversive conditioning and reducing elk forage attractants. However, compared to the demonstrated effectiveness of wolves, these methods may do little in isolation to change elk population size in the central zone.

Wolves recolonized the eastern zone in 1992/93, however, habitat fragmentation caused by the TCH and an open waterway associated with a hydroelectric development (the Penstock) restricted full wolf use of the eastern zone. The Penstock was buried in 1995/96, and wolves increased use of the eastern zone north of the TCH dramatically (Stevens and Owchar 1996, chapter 4, Fig. 1), and this appeared to relate to elk declines after 1995/96 (chapter 4, Fig. 4). Duke et al. (in press) report similar effects of corridor restoration on Cascade pack movements and kill-rate north of the TCH in the central zone during 1997/98. Therefore, corridor restoration in existing urban landscapes, and appropriate urban planning which considers carnivore corridor use in new developments is essential to reduce or preventing development of urban elk populations.

Although human-caused mortality was not a good predictor of elk population growth rates, human-caused mortality is likely an important limiting factor of elk population growth. Fencing the TCH in the central zone resulted in a large increase in central zone population growth rates. In the western zone, human-caused mortality rates were relatively high (table 3, chapter 4). Cause-specific mortality rates for elk will help us to understand the role of human-caused mortality (McKenzie, in prep.).

Implications for Wolf-Elk Dynamics

The effects of wolf predation on elk populations will depend in part on whether wolf predation is described by a type II or type III functional response (Holling 1959, Messier 1995b). I will estimate the shape of the functional response for wolves in BNP using data from this thesis in future research (Hebblewhite, in prep.). However, I believe my research suggests the functional response should be type II. The importance of elk to wolf kill-rates (chapter 3) suggests wolves will not switch between elk and other prey at low elk density. This is similar to wolf-caribou-moose dynamics (Dale et al. 1994, Dale et al. 1995), characterized by a steep type II functional response for wolves preying on caribou.

The effects of herding on predation by wolves in chapter 2 suggests more similarities to wolf-caribou dynamics. Wolves have higher encounter rates and attack success on larger herds of elk, and I predict increased predation rates of elk at intermediate elk densities, leading to a steeply shaped type II functional response than when compared to wolf single-prey models (i.e., moose-wolf, Messier, 1994).

The effects of alternate prey on predation rates by wolves on elk could result in a numeric response of wolves to elk with a positive Y-intercept, because alternate prey could sustain wolves in the absence of elk (Messier 1995b). In simulation models, Messier (1995b) showed a type II functional response combined with either a linear or type II numeric response with a positive Y-intercept lead to total predation rates on elk that are depensatory, or highest at intermediate-low densities (Messier 1995b). The dependence of wolf kill-rates on elk in chapter 3 suggests a numeric response through the origin. In this case, a type II wolf functional response would lead to predation rates that are density-dependent (Messier 1995b). In the presence of other predators, numeric responses with and without a zero Y-intercept may both result in low-density elk populations (Messier, 1995b).

Regardless of the nature of the wolf predation rate on elk, empirical evidence from chapter 4 demonstrates the limiting role that wolf predation has on elk populations in BNP. The effects of wolf predation on elk we observed are from an exploited wolf population, therefore the numeric response of wolves to prey density was likely depressed. Total predation rate possible for an unexploited wolf population should be higher than we observed.

Conservative ungulate harvest management may therefore be required, especially during early wolf recolonization as a result of these many factors. Wolf kill-rates on elk may be increased at high elk density due to wolf-elk herding relationships. Wolves may have higher survival and recruitment, and therefore predation rates, during early recolonization when compared to long-term conditions. Post-wolf restoration harvests of ungulates should be expected to be less than pre-wolf restoration, precipitating conservative harvest management in areas where wolves are recolonizing to ensure the long term sustainability of wolf-elk-human hunter systems.

My research suggests that wolves are important ecologically, potentially functioning as keystone species in montane ecosystems through their effects on elk populations. Collaborative research in BNP suggests a mechanism of increased predation on elk reducing elk density, with increases in willow, aspen and other vegetation in response to reduced herbivory by elk. By reducing competition with elk for these plant resources, wolf predation may indirectly benefit moose, beaver, and biodiversity in general. Future research in BNP should formally test this hypothesis.

The strength of the effect of wolf predation on elk populations suggests hunting ofelk by humans may not be necessary to achieve ecological integrity objectives in BNP. Invoking the need for hunting by humans to remedy the lack of aspen regeneration in response to the restoration of wolf predation (White et al. 1998, White 2001) may be preliminary, especially considering the exploited nature of wolf predation in the Bow Valley of BNP. Evidence for elk densities that are almost low enough to regenerate aspen clones in the Bow Valley of BNP within 15 years of predation by exploited wolves suggests that hunting by humans is not necessary to maintain and restore ecological integrity in BNP. This should be an attractive implication for managers because it precludes opening up the Pandora's box of hunting by humans in National Parks, and adheres to the Parks Canada principle of using minimal human interference to achieve ecological integrity objectives. While hunting by humans was no doubt important in shaping ecosystem states, uncertainty over effects of native hunting before and after the introduction of firearms and horse-based hunting, as well as the difficulties in quantifying overall impacts of hunting, make science based management that includes a role for hunting by humans difficult, especially in today's realities of increasing human habitat fragmentation and habitat loss in and around our National Parks.

Conclusions

Management interpretation of the effects of wolf predation on elk populations will differ dependent on the policies of the responsible land management agency. In National Parks and other protected areas mandated with the maintenance and restoration of ecological integrity, the impact of predation by wolves on elk populations should be viewed in a positive frame of mind. Wolf restoration should resolve long-standing debate about the management of ungulate populations that are perceived by some as being “overabundant” (Kay 1998, Boyce 1998, Singer et al. 1998), and will assist National Park objectives of maintaining biodiversity due to the positive effects of predation by wolves on ecosystems suggested by my research.

However, in management environments where the production of a maximum sustained yield of elk or other ungulates for the hunting and/or the guiding industry is an important management objective, the implications of my research may be interpreted quite differently. Managing carnivores such as wolves differently in adjacent land management agencies is difficult (e.g., Smith et al. 1999). Wolves are susceptible to human-caused mortality due to their large home ranges, vagile nature, and potential for conflict with humans via livestock depredation (reviewed in Noss et al. 1996, Weaver et al. 1996). Therefore, wildlife managers should note the ecological importance of wolves regardless of management environment on an appropriate ecosystem scale.

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