THE ECOLOGY OF GRAY WOLF (*Canis lupus*) HABITAT USE, SURVIVAL, AND PERSISTENCE IN THE CENTRAL ROCKY MOUNTAINS, CANADA

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ABSTRACT

THE ECOLOGY OF GRAY WOLF (*Canis lupus*) HABITAT USE, SURVIVAL, AND PERSISTENCE IN THE CENTRAL ROCKY MOUNTAINS, CANADA

Carolyn Joann Callaghan
University of Guelph, 2001 Advisors: Drs. D. M. Lavigne and T. D. Nudds

I examined the combined effects of topography and anthropogenic activity on habitat use, survival, and population viability of gray wolves (*Canis lupus*) in the Central Rockies between 1987 and 2001. Although large protected areas exist in the region, the territories of few wolf packs occur wholly within them. Most wolves in the population are exposed to mortality risks from hunting, trapping, or automobile collisions. Moreover, their low population density raises concerns about anthropogenic effects on population persistence.

I built multivariate habitat use models using winter snow tracking data from four wolf packs, digital data on habitat characteristics, and multiple regression analyses. Data were pooled to produce a regional habitat use model and compare habitat use at different scales. Elevation was a strong predictor of wolf habitat use. Predictor variables differed between regional and pack models, indicating that the models were sensitive to scale.

I investigated survival rates and causes of mortality for 31 radiocollared wolves from 12 packs. Poisson regression was used to assess the effects of eight independent variables. Human-caused deaths constituted 75% of total mortalities and most (67%) of human-caused mortalities occurred outside of protected reserves. Wolves survived longer in

territories protected by reserves than in territories spanning reserves and non-protected areas. Hunting activities were negatively associated with wolf survival.

I used snow-tracking data from four wolf packs over 6 winters and General Linear Models to investigate response of wolves to linear features including roads, rivers, and compacted trails. The proportion of successful crossings did not differ among type of linear feature, but differed among road type. Wolf deaths per km differed among road types.

A population viability model was used to investigate interaction of wolf social dynamics and population parameters. Simulations indicated low probability of extinction under current conditions. Population carrying capacity, number of immigrants, maximum litter size, and severity of catastrophe accounted for the greatest variability in probability of extinction. Protected areas within the region are too small to maintain population persistence without relying on immigrants from outside of protected reserves. To ensure wolf population persistence, a coordinated approach to regional wolf management is recommended.

For Steve and Madeline,

And

For Aster, Betty, and Nakoda – the matriarchs of the Central Rockies wolf population.

ACKNOWLEDGEMENTS

My committee has referred to me on several occasions as an unusual student. Dave Lavigne once called me an anachronism for my interest in natural history during an era of technological worship. Most students get to their studies, complete them in due time and get on with their lives and careers. Not Callaghan. She decides to make the thesis a part of a life's work by establishing an organization for wolf research and conservation, having a child, continuing to write funding proposals and coordinate field work while writing her thesis – indeed, even expanding the project to southern Alberta where the focus is on reducing conflicts between wolves and ranchers. In retrospect, I must have been mad. The compulsion to continue this work is an affliction from which I will not easily recover.

Somewhere between the impossible and the inevitable, the thesis was completed. Any endeavour of this magnitude, however, is not successful without the important role of many organizations and individuals. The list of people whose support was critical to the project is staggering. Parks Canada and Alberta Environment were instrumental in supporting the research from a logistical and funding perspective. The Banff National Park Warden Service had the foresight to initiate wolf research in the park in the mid 1980s. In particular, Tom Hurd, Alan Dibb, Derek Petersen, Cliff White, Mike Gibeau, and Dave Dalman are to be commended for considering wolf research to be an important component of their management program. Parks Canada provided logistical support by providing equipment, research vehicles, a research lab, necropsy facilities and the support of a wildlife veterinarian, spatial data, use of backcountry cabins, the support of an expert public safety team, aerial telemetry and aerial transportation, and the support of wardens and dispatch personnel. Martin Urquhart, A.L. Horton, Dave Norcross and Tom Davidson provided much of the logistical support required to meet our daily research needs in Banff National Park. Tom Hurd provided data on elk densities and wolf mortalities. Pierre Chambfort provided traffic data. Dave Gilbride and Darrel Zell provided GIS assistance. Don Gorrie provided expertise on trail use by humans in Banff, Kootenay, and Yoho National Parks. Thanks also to Tim Auger, Mark Ledgewick, the dispatch staff, and Alpine Helicopters for being a great mountain rescue team and developing a safety system that provided assurance to us on our back-country trips. In addition to providing support for the project, Parks Canada managers included me and the collection of wolf researchers in management workshops in effort to inject the most recent scientific knowledge of wolves in the management decision-making process.

Alberta Departments of Sustainable Resource Development and Community Development also played a critical role in supporting our research. Steve Donelon, Jon Jorgenson, and Dave Hanna are unfailingly supportive of wildlife research in Kananaskis Country. They provided housing, vehicles, aerial telemetry support, volunteers, funding to hire staff, equipment, the support of an expert public safety team, and spatial data. Peter Lougheed Rangers Jay Honeyman and Randy Axani provided the support to meet our daily research needs, and all of the Park Rangers and Fish and Wildlife Officers provided assistance at one time or another. George Field provided us with avalanche safety training. Peter Kilburn, Alberta Transportation, provided traffic data. Alberta

Environment managers also sought our involvement in management decisions that had potential effects on wolves.

Bob Forbes and Bill Warkenton, British Columbia Ministry of Environment, provided information on elk densities and wolf mortalities. The staff at Elk Lakes Provincial Park and Mount Assiniboine Provincial Park provided logistical support for field work. Dr. Todd Shury provided excellent veterinary services and advice on animal care. Drs. Dave Brace, Pillar Gosselin, Silvia McAllister, and Mark Johnson also willingly provided veterinary services and advice over the years.

I consider myself to be very lucky to have had competent and enthusiastic field assistants over the years. Anyone who has conducted winter field studies in northern climates can attest to the fact that this type of work is very challenging. My study animal provided the additional challenge of trying to keep up with very efficiently travelling quadrupeds. A wolf pack can easily travel 60 km in a day. We estimated that it takes us 4 days to travel the distance on foot or skis that a wolf pack typically travels in one day. Add the complexity of very rugged topography and a small flying budget, and you may begin to understand that every piece of data collected took sheer determination. Beyond the winter data collection, summer radiotelemetry data collection often entailed standing at the shoulder of busy highways and concentrating on listening to the signal while traffic whizzed past. It is a wonder that anyone stayed on longer than one season, but several did. In fact, 7 of my research assistants took on a graduate project of their own. A common thread among field assistants was a love for the outdoors and for the conservation biology of wolves. I am grateful to all who contributed directly to the data collection during my tenure as a graduate student, including Shelley Alexander, Steve Anderson, Sheila Antonation, Connie Atkinson, Bettina Bannes-Grewe, Barb Bertch, Gunther Bloch, Karin Bloch, Stacey Ciancone, Brenda Dobson, Matt Dragon, Danah Duke, Chris Darimont, Sarah Goulet, Mark Hebblewhite, Otso Huitu, Sharon Irwin, Barb Johnston, Karen Lassen, Melissa Mauro, Cam McTavish, Cedar Mueller, Peter Nawrath, Chuck Newyar, Bridget McClarty, Melanie Percy, Jens Persson, Doerte Possig, Danielle Robertson, Joanne Saher, Pete Smillie, Yoshinori Sotei, Gabriella Stupekoff, BJ Stewart, Alex Taylor, Martin Urquhart, Erin Urton, Joep Van der Vlassiker, Mike Vassal, Joachim Vos, Jen Wasylyk, and Jesse Whittington.

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Flying in mountainous terrain comes with its own set of challenges, as John P. can attest to following his emergency landing on Highwood Pass. I am grateful to Mike Dupuis, Mike Gibeau, John Paczkowski, Martin Urquhart, Saundi Stevens, Jon Jorgenson, and Mark Hebblewhite for collecting aerial telemetry data. Mike Dupuis of Wildlife Observation Service, Calgary, proved to be an excellent fixed-wing pilot and wildlife observer. Alpine Helicopters provided expert aerial support for radio telemetry and aerial darting. Thanks to Lance Cooper for overseeing and safely piloting much of the aerial support.

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I owe my academic committee a debt of gratitude for taking me on as an apprentice. Each of them is a good role model in conservation biology, and all have influenced my way of thinking and contributed to my understanding of the role of science in decision-making. I am grateful to DML for seeing the potential and offering a helping hand when I needed it, for folding me into the IMMA umbrella, and for scrounging up funding for my project. I admire Dave for not being afraid to make the leap to what is considered by some to be the other side, for understanding the importance of choosing a path that makes you happy, and for his insights into human behaviour. A recent opportunity to observe Dave as the rapporteur of a scientific conference reminded me of the wisdom of the mentoring process. I thank Tom for grounding me in the scientific method, for challenging my conservation paradigms, and for understanding the importance of reprioritizing one's life when very important events happen (even if it means he is branded as a new age professor). Tom was also a good sport to take me under his wing when Dave left the University of Guelph and was readily available when I needed him for those oh-so-difficult discussions about statistical methods over the telephone. Tom and Dave inspired me to become a better writer through their excellent editing skills. Vern imparted many jewels, not the least of which is "humans have a cultural veneer with a biological core." He also provided me with some very sound advice that I did not heed -- to complete my thesis as quickly as possible because no one receives a gold watch for graduate studies. Paul is a wonderful mentor and fellow traveller in the world of wolves and dogs. He laid the foundation upon which I and other graduate students could help to build an ecological understanding of wolves in mountainous systems. I thank him for helping me to understand the importance of humans in the conservation equation, for being a well-rounded person, for not being afraid of mixing emotions with science, and for approaching conservation with unfailing integrity. Paul's support and encouragement throughout the process was a candle of warmth. I also thank Mary Anne Davis for administrative support (You mean I haven't paid my tuition fees yet?). Beren Robinson provided critical advice on the statistical analysis of Chapter 4.

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Thank you to Farley Mowat for the early inspiration. Thanks also to John Theberge for introducing me to the world of wolves.

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CHAPTER ONE

GENERAL INTRODUCTION

The wolf population in the Central Rocky Mountains was extirpated or severely depleted twice during the 20th century (Paquet 1993). Wolves were very scarce by the early 1900s, and most were eliminated by 1914 (Cowan 1947). Natural recolonization occurred during the 1930s (Cowan 1947) and, by the 1940s, full reestablishment of the population was believed to have occurred (Green 1951). Extensive predator control programs in Alberta, British Columbia, and the four mountain national parks during the 1950s again severely reduced or eliminated the wolf population in the Central Rockies (Ballantyne 1956; Gunson 1992; Mickle et al. 1986; Tompa 1983).

In the decades following wolf culling, public attitudes toward wolves became more positive (Kellert 1985), and governments' management regimens followed suit. A natural recolonization of wolves occurred in the Central Rockies between the mid-1970s and the early 1990s (Holroyd and Van Tighem 1983; Paquet 1993; Parks Canada unpublished data). Evidence of breeding wolves was recorded in the Panther and Clearwater Valleys of Banff National Park in the mid-1970s (Holroyd and Van Tighem 1983). Other areas, such as the Bow Valley watershed and Kootenay and Yoho National Park did not support breeding wolves until the early to mid-1980s (Mickle et al. 1986; Poll et al. 1984). By the mid 1990s, twelve packs had become established in the study area (Paquet and Callaghan unpublished data).

In 1987, Banff National Park initiated wolf research in the Bow Valley. Park managers were most interested in understanding how an apex predator would fit into a system rich with 7 large ungulate species and 6 sympatric carnivore species. Dr. Paul Paquet was contracted by Parks Canada to oversee the wolf research program, and he expanded the study area to include approximately 18,670 km^2 of the Central Rockies (Paquet 1993). Within that area, 9 wolf packs were studied intensively and information was gathered to the fullest extent possible on 3 other packs. Since 1987, some packs disintegrated, several territories increased in size, and a few new packs have formed. Figure 1.1 shows the approximate locations of 12 packs currently in the study area.

Early research on wolves in the Central Rocky Mountains hypothesized about the limitations imposed by mountainous terrain on wolf movements (Green 1951; I. Cowan, pers. comm.). More recent investigations in the region proposed hypotheses consistent with this early research. Distribution of prey, influenced by physiography, was believed to affect wolf movements during winter (Huggard 1991; Purves et al. 1992). Paquet (1993), Alexander et al. (1996) and Paquet et al. (1996) conducted preliminary investigations of wolf habitat use. Research on wolves in other areas of the Rocky Mountains or in other mountain systems similarly investigated wolf-habitat relationships (Singleton 1985; Boyd-Heger 1997; Kunkel 1997; Massolo and Meriggi 1998; Ciucci et al. 2000). Compacted trails and roads have been recognized to be both beneficial and detrimental to wolves in other areas (Formozov 1946; Green 1951; Mech 1970; Zalozny 1980;

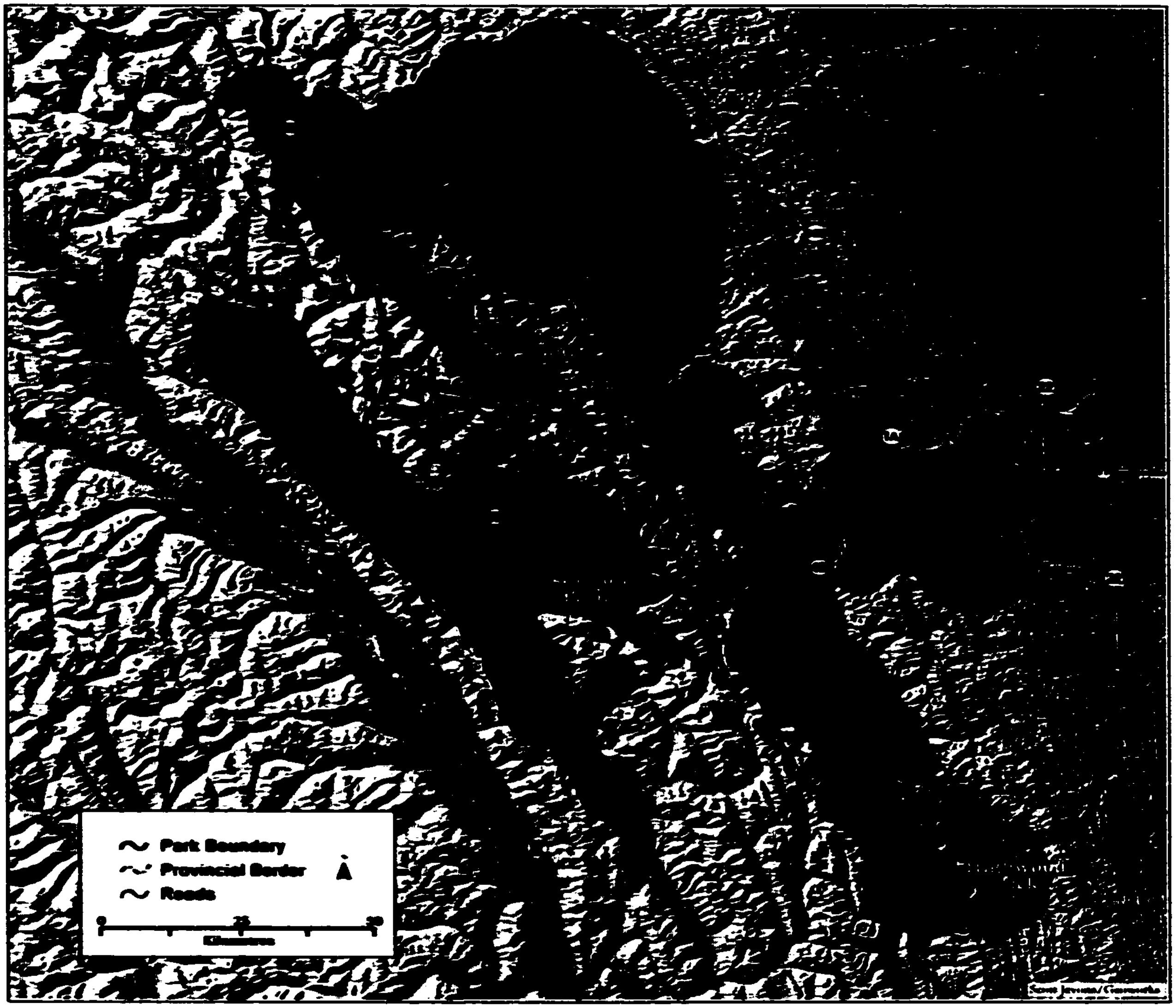

Figure 1.1. Location of the study area in the Central Rockies showing approximate territories for twelve wolf packs in the region, 2001.

Bjarvell and Isakson 1982; Paquet 1993; Van Ballenberghe et al. 1975; Berg and Kuehn 1982; Fuller 1989; Mech 1989). Human activities in Banff, Kootenay, and Yoho National Parks predominate in montane habitats that were considered to be of high quality for wolves and displacement of wolves from areas of high human use in valley bottoms was documented by Purves et al. (1992). The effects of anthropogenic activity on wolf habitat use did not receive rigorous evaluation, however. Thus, the need for a spatially realistic analysis of wolf habitat use and movement patterns was recognized in 1995 by the Bow Valley Task Force (Green et al. 1996). This thesis provided an excellent opportunity to investigate the specific landscape variables associated with wolf habitat use and the effects of human activities on wolf movement patterns in mountainous habitats.

Elevation and topography throughout the Central Rockies contribute to a highly variable climate. The complex climate regimen is evidenced by the distribution of plants and animals in the study area (Janz and Storr 1977). Such natural patchiness of mountainous habitat likely reduces the environmental carrying capacity (K) of wolf populations. Annual mid-winter population surveys in 18,670 km^2 of the Central Rockies during 1997 – 2000 indicate a population of approximately 60-70 wolves (Callaghan and Paquet unpublished data), or 3.2 – 3.7 wolves per 1,000 km^2. Removing elevations and slopes that wolves do not use in the study area (>2451 m and >66°) in a geographic information system resulted in a total area of 15,381 km^2, which translates to a density of 3.9 – 4.6 wolves per 1,000 km^2. A comparison to wolf population densities in North America (2.7 – 41.7 wolves per

1,000 km^2) reported by Keith (1983) suggests that the Central Rockies wolf population exhibit among the lowest densities of wolves in North America.

The Central Rockies wolf population is exposed to hunting and trapping pressure, livestock depredation control, automobile collisions, and recreational development. Although wolf packs using protected areas such as national and provincial parks are protected from hunting and trapping, few home ranges exist solely within a protected area. Furthermore, although wolves are considered to have relatively high resilience to anthropogenic effects due to a high reproductive rate and a capability of dispersing over broad areas (Weaver et al. 1996), mountainous habitat may impose limits to such resilience (Carroll et al. 2000). Human activity in the Central Rockies has increased markedly over the past decade, and is projected to continue increasing (Pacas 1996; Carroll et al. 2000), raising concerns about anthropogenic effects on habitat use and survival of wolves in the Central Rockies (Paquet et al. 1996; Callaghan et al. 1998).

A viable wolf population requires habitat with adequate prey and refuge from overexploitation by humans (Fritts and Carbyn 1995). The population dynamics of wolves are also affected by complex social behaviour and dispersal patterns (Vucetich et al. 1997), which may have important implications for population persistence. Although the social behaviour of species and their response to human activities can have important implications for population viability (Tuyttens and MacDonald 2000), few attempts have been made to understand the relationship between behaviour and persistence (Durant 2000).

The objective of this thesis was to investigate the combined effects of the topographical restrictions imposed on wolf habitat use, anthropogenic effects on habitat use and survival, and behavioural elements of wolf biology on the persistence of the Central Rockies wolf population. The second chapter of the thesis builds on preliminary analyses of wolf-habitat relations in the Central Rockies by Paquet (1993), Alexander et al. (1996), and Paquet et al. (1996) using a multivariate analysis of wolf habitat use in winter. The third chapter is an analysis of wolf survival in the Central Rockies. The fourth chapter investigates of the influence of linear features on wolf movements in winter and of the relationship between automobile traffic volume and wolf mortality. In the fifth chapter, a population viability model is used to conduct a population viability analysis of wolves in the Central Rockies. The sixth chapter is a synthesis of chapter two to four.

I show that topographical and climatic factors restrict wolf movements to low elevation areas in the Central Rocky Mountains and that wolves, humans, and elk converge in low elevation areas during winter. Landscape modifications by humans in low elevations provide compacted trails and roads that wolves are both attracted to and repulsed from. Such modifications have implications for predator-prey relations and wolf survival. Conflicts between wolves and humans along edges of reserves reduce wolf survival and contribute to the reliance on immigrants from unprotected areas of the region for population persistence. The current protected areas are not large enough to maintain a viable wolf population in the Central Rocky Mountains without immigration.

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CHAPTER TWO

A HABITAT USE MODEL FOR WOLVES IN MOUNTAINOUS TERRAIN

INTRODUCTION

Managing for the persistence of wildlife populations requires an understanding of environmental conditions that affect the distribution and abundance of populations. Understanding environmental factors that determine wildlife population trends also facilitates predicting the effects of human activities on population persistence (Morrison et al. 1998).

Habitat is described as "the locality, site and particular type of local environment occupied by an organism" (Lincoln et al. 1998). Selection is implied through the disproportionate use of a resource relative to its availability (Manly et al. 1993). It is likely impossible, however, to understand how animals perceive their environment. Thus, decisions by researchers on what constitutes habitat availability affect inferences about habitat selection (Thomas and Taylor 1990). Johnson (1980) described habitat selection as occurring via a series of choices made in a hierarchical fashion at various spatial scales, from species' range to home range selection to within home range habitat selection. The criteria for habitat selection may vary among spatial scales, thus study design and inference of habitat use patterns should reflect a hierarchy of habitat selection (Manly et al. 1993). Herein, I use the term habitat selection to denote that some habitat types are used disproportionately more or less than if animals chose habitats randomly.

Few studies use contiguous snow tracking to collect habitat use data (Oksanen et al.

1992; Storch et al. 1990; Bateman 1986; Richardson et al. 1987; Snyder and Bissonette 1987; Singleton 1995). Contiguous tracking provides more detailed information of animal movements than most radio-telemetry studies can provide, including areas of concentrated use, avoidance behaviour, interspecific interactions and use of movement corridors (Carbyn 1983; Paquet 1992; Musiani et al. 1998).

Throughout its broad geographical distribution, the gray wolf is considered to show low habitat affinity and therefore is regarded as a habitat generalist (Mech 1970; Fuller et al. 1992; Mladinoff et al. 1995). In the Rocky Mountains, however, the effects of topography and climate concentrate activities of some species into forested valley bottoms (Holland and Coen 1983; Paquet 1993; Apps 1996; Paquet et al. 1996; Carroll et al. 2000). The narrow, linear valley bottoms, separated by steep, rugged mountain ranges, create a mosaic of natural patchiness (Paquet 1993; Paquet et al. 1996; Callaghan et al. 1998). Wolves also respond to movements of their primary prey, using montane valleys during winter, and increasing their range to subalpine habitats during summer (Paquet 1993). Wolves may therefore exhibit affinity to certain habitats in mountainous terrain.

It is generally assumed that wolf habitat preference is strongly related to availability of prey (Holroyd and Van Tighem 1983; Huggard 1991). Few studies, however, have quantified wolf habitat use. Several studies have investigated habitat features associated with den site selection (Joslin 1966; Mech 1970; Clark 1971; Stephenson 1974; Carbyn 1974; Ballard and Dau 1983; Ream et al. 1989; Ciucci and Mech 1992; Heard and Williams 1992; Matteson 1992) and how snow depth (Nelson and Mech 1986; Fuller

1991) and road density (Thiel 1985; Thurber et al. 1994; Edmonds 1988; Fuller 1989; Jensen et al. 1986) are linked to wolf habitat use. Recent studies have investigated the influence of landscape and anthropogenic factors on wolf colonization or habitat use in relatively homogeneous landscapes (Mladinoff et al. 1995; Mladinoff et al. 1997; Haight et al. 1998; Mladinoff and Sickley 1998; Mladinoff et al. 1999).

Mountainous habitat is naturally patchy, and human activities tend to concentrate in the montane mountain habitats (Paquet et al. 1996). The combined effects of topography and anthropogenic activities may limit use of montane areas by wolves. Alternatively, wolves may benefit from packed roads and trails and exploit habitats from which they would normally be excluded in deep snow conditions. Although previous research on wolves in the Rocky Mountains hypothesized about the limitations imposed by mountainous terrain on wolf movements (Green 1951; I. Cowan, pers. comm.; Huggard 1991; Purves et al. 1992) or investigated the univariate relationships between habitat features and wolf movements (Paquet 1993; Alexander et al. 1996), few studies have investigated the combined effects of topography and anthropogenic activity on wolf movements (Singleton 1995; Paquet et al. 1996; Boyd-Heger 1997).

Broad scale predictive models have been applied to wolf habitat use in homogeneous landscapes (Mladinoff et al. 1995; Mladinoff et al. 1997; Haight et al. 1998; Mladinoff and Sickley 1998; Mladinoff et al. 1999), and other research has demonstrated an attraction to roads by wolves for travel routes (Formozov 1946; Green 1951; Mech 1970; Zalozny 1980; Bjarvell and Isakson 1982) or a repulsion from areas of high road density

(Mladinoff et al. 1997; Mladinoff et al. 1999). The complex topography of mountainous terrain constrains roads to the valley bottoms, and in mountainous terrain, wolves may have little choice of travel routes, but little is known of the response of wolves to roads in such circumstances. Wolves that avoid roads in mountainous habitats may not find alternate routes to access prey, and wolves that use roads for travel routes are exposed to a potential source of injury or mortality via collisions with automobiles or exposure to hunters who use roads. To test whether roads and trails influence wolf use of mountainous terrain, I built multivariate habitat use models for four wolf packs in the Central Rocky Mountains using a Geographic Information System (GIS), digital data on landscape and anthropogenic characteristics, snow tracking data collected between the winters of 1994 – 1996, and multiple logistic regression analyses. I examined whether habitat models developed at the home range level could be applied accurately over a larger landscape by pooling the data to produce a regional habitat use model and testing the predictive capability of the model using snow-tracking data that was not applied to develop the model.

STUDY AREA

The present study was conducted in portions of Banff National Park, Alberta and Kootenay, and Yoho National Parks, British Columbia between 01 November and 31 March in 1994-1995, 1995-1996 and 1996-1997. The area covers 4,185 km^2 and is located in the Continental Range of the Central Canadian Rocky Mountains, spanning the continental divide and centring on approximately 50° 59' 52.84" N 115° 58' 54.99" W.

The study area encompasses the headwaters of three major rivers: the Bow, Kickinghorse and Kootenay Rivers (Figure 2.1).

Topographic features of the study area include rugged mountain slopes, narrow, steep-walled tributary valleys, and broad main valleys. Elevations range from 1040 m to 3520 m. Most vegetation occurs along the valley bottoms and lower mountain slopes and shoulders. Three ecoregions are found within the study area: the montane, subalpine and alpine (Holland and Coen 1983). The montane ecoregion is dominated by lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea* sp.) and aspen (*Populus tremuloides*) interspersed with grassy slopes, meadows, and wetland complexes. The subalpine ecoregion is dominated by lodgepole pine, Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) forest and open spruce, wetland-shrub meadows. Low shrub and herb communities characterize alpine areas. Avalanche slide paths are common in the subalpine and alpine regions of the study area, where vegetation consists of a mosaic of shrub and herbaceous species, including slide alder (*Alnus crispa* sp.*)*, and cow parsnip *(Herqcleum lanatum)*.

Precipitation increases with increasing elevation. Mean annual precipitation for the area ranges from 468.0 mm at 1400 m above sea level in the Bow Valley (Banff National Park Warden Service) to 687.7 mm at 4100 m above sea level at the Yoho National Park Warden Compound (Yoho National Park Warden Service).

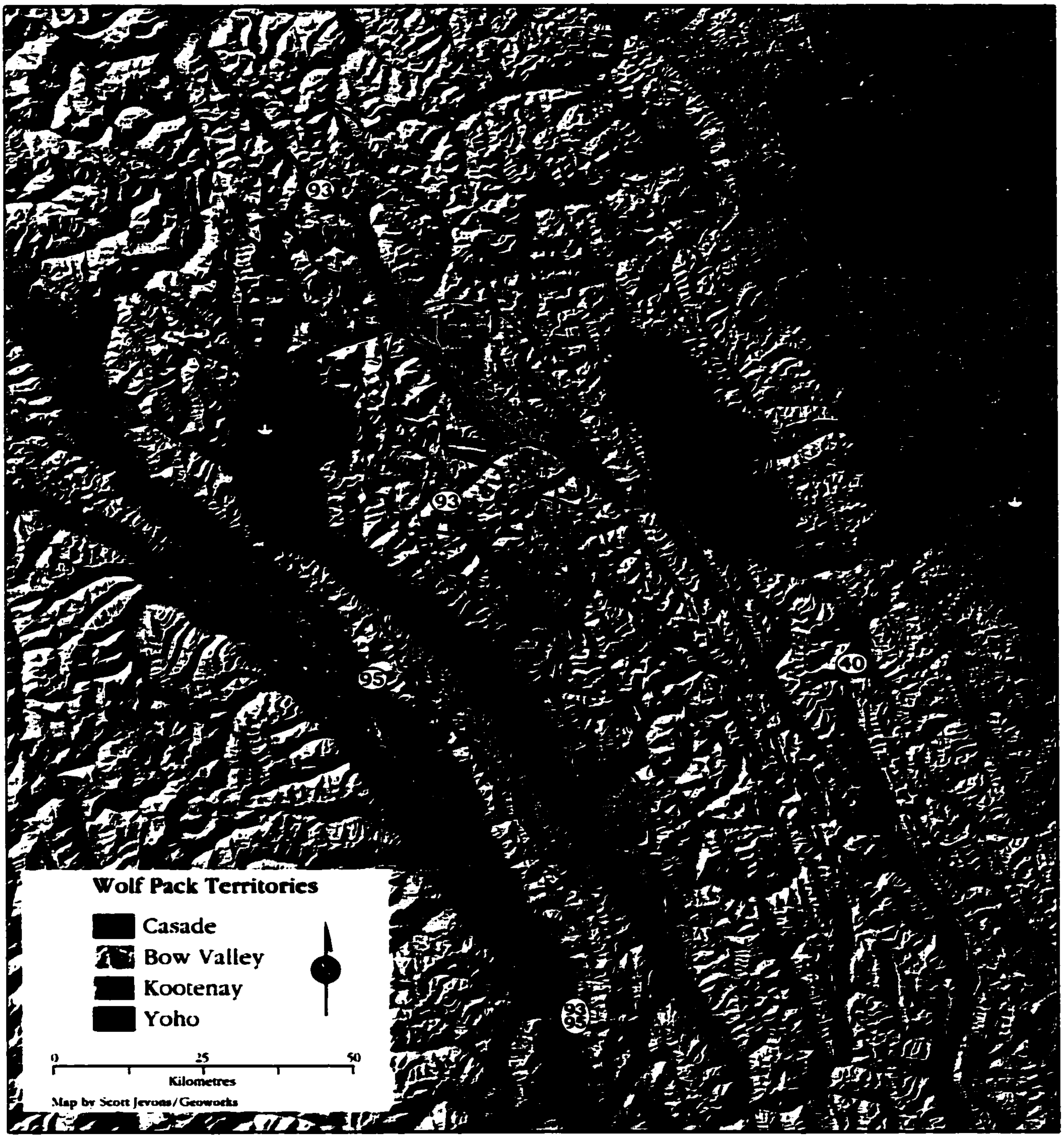

Figure 2.1. Study area showing the 95% isopleth adaptive kernel home range of four wolf packs.

Seven large ungulate species occupy the study area (Holroyd and Van Tighem 1983), including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), and mountain caribou (*Rangifer tarandus).*

Small towns, roads and human developments are scattered throughout the study area. Settlements occur within and outside of protected areas (Figure 2.1). The town of Banff has a resident population of approximately 6,000, and the hamlet of Lake Louise has a resident population of 1,500. Two major transcontinental transportation routes, the Trans Canada Highway (TCH) and the Canadian Pacific Railway (CPR), traverse the Bow River Valley of Banff National Park and the Kicking Horse Valley of Yoho National Park. A secondary highway (Hwy 93) bisects Kootenay National Park and the portion of Banff National Park north of Lake Louise, and a secondary highway (Hwy 1A) bisects a portion of the Bow Valley in Banff National Park. Average daily traffic volume during the winters of the study period was 6,009 automobiles on the TCH (Redearth Creek Counter), 1,090 automobiles on Hwy 93 (Storm Mountain Counter) and 211 automobiles on Hwy 1A (BVP East Monitor) (Public Works Canada unpublished data). An extensive network of hiking, skiing and equestrian trails exists within the study area. Other facilities include downhill ski areas, picnic areas, campgrounds, a golf course, an airfield, and horse barns.

METHODS

Data Collection

I collected snow-tracking data from four wolf packs in the Central Rocky Mountains between November 1 and April 30, 1994 to 1997 (Figure 2.2). Because wolves are social animals and individuals in a pack exhibit relatively cohesive movement patterns, the important ecological unit is the pack. Further, to avoid problems of pseudo-replication, my analyses are at the pack level rather than at the individual level. The Cascade and Bow Valley packs exist primarily within Banff National Park; the Kootenay pack exists within Kootenay National Park and adjacent crown land in British Columbia; and the Yoho pack exists within Yoho National Park and adjacent crown land in British Columbia (Figure 2.1). When possible, wolves were snow-tracked on a daily basis throughout each winter. Trackers travelled via snowshoes or skis. Fresh wolf tracks were backtracked to minimize disturbance to our study animals. Tracking sessions were continued for consecutive days until snowfall, lack of snow, or avalanche hazard precluded tracking. Global Positioning System (GPS) units were used to collect waypoints as Universal Transverse Mercator (UTM) coordinates along tracking session lines. The data were imported to a GIS (Idrisi, Clark University 1987) and entered into a database file. A total of 2,437 km of tracking data from 818 tracking sessions was used to derive sample points for the model (580 km from the Bow Valley pack, 1131 km from the Cascade pack, 347 km from the Kootenay pack, and 379 km from the Yoho pack). Radiocollars were fitted on one or more members of each wolf pack prior to and during the study period. Wolves were captured for radiocollaring using aerial darting, aerial net gunning, or using steel leg-hold traps modified for research purposes. Capture and

Figure 2.2. Travel routes of four wolf packs recorded over three winters between 1994 and 1997.

immobilization methods are detailed in Paquet (1993). A total of 14 wolves from the four packs were fitted with radiocollars (Lotek Engineering, Newmarket Ontario) during the study period. When possible, radiocollared wolves were relocated on a daily basis via ground telemetry and via aerial telemetry when the study animals could not be located through ground telemetry. GPS units were used to fix aerial locations and observer position for ground telemetry. Telemetry location error was estimated using stationary transmitters placed throughout the study area. Estimated mean error of location was 225 m $\pm$ 75.3 m (SD) at 500 m. Radiotelemetry locations were analyzed at the pack level, thus data from more than one radiocollared animal per pack were pooled. One location per day was selected randomly from the data for home range analyses.

Map Layers

Digital data available for spatial analysis were obtained from Parks Canada, and included information on topography, vegetation, prey habitat, hydrology, roads and trails (National Topographic Database Series, Ministry of Supply and Services Canada 1986 and Geomar Consulting). I compiled twelve spatial data sets of biophysical or anthropogenic attributes describing wolf habitat in the study area at a resolution of 30 m x 30 m: elevation (ELEV), aspect (ASP), slope (SLP), terrain ruggedness (TRUG), prey habitat quality (PREY), hiding cover (HIDE), snow shedding (SNOW), distance from high use (RDHI) and low use (RDLO) roads, distance from high use (TRHI) and low use (TRLO) trails and distance from water (WATER).

Elevation, aspect, slope, and terrain ruggedness layers were derived from a Digital Elevation Model (DEM) for the region at a scale of 1:50,000. Aspect was transformed to a continuous variable for the logistic regression model (Beers et al. 1966). I used a terrain ruggedness index that was developed with a moving window technique within a 1 km grid. TRUG indexes complexity of terrain, and was derived using the following equation:

$$TR = (De * Ac)/(De+Ac),$$

where De = density of contour lines within a given window and Ac = an index of aspect variability within a given window. (Wierzchowski unpublished data).

I generated a prey habitat suitability layer using an Ecological Land Classification System (ELC) (Holroyd and Van Tighem 1983) for the four-mountain national parks biophysical inventory at a scale of 1:50,000. The ELC classifies and integrates landform, soil, vegetation, and wildlife information in map format. The units of description include ecosites, which are classified according to soil and vegetation physiognomic and floristic components, and are the mapping units of the ELC (Holroyd and Van Tighem 1983). I derived prey habitat suitability from the ELC, which ranks the relative importance of each ecosite to ungulates based on pellet, ground and aerial surveys, and snow tracking. Although Holroyd and Van Tighem (1983) classify habitat quality into four categories (low, moderate, high, very high), I combined high and very high quality into one category (high) and included a non-habitat category. To create the prey layer, I used an equation that ranked the relative importance of each prey species to wolves using data collected from 649 wolf kills in the study area between 1987 – 1997 (Paquet and Callaghan unpublished data; Table 2.1). Biomass estimates were weighted according to mean mass of species, age, and sex of identified kills as per Weaver (1994). The relative importance of each prey species in wolf winter diet was used to combine the spatial layers for elk, moose, deer, bighorn sheep, and mountain goats into one prey layer (Table 2.2).

Wolves may use habitat types that provide hiding cover to reduce detection by humans or prey. Wolves may also use vegetation types that retain snow, which reduces snow depth on the ground thus increasing efficiency of movement. I thus generated a hiding cover layer and a snow shedding layer using a landsat satellite-derived land cover image (Geomar Consulting). I combined the vegetation categories into five classes (Table 2.3) to derive the hiding cover layer and three classes to derive the snow-shedding layer (Table 2.4).

Road and trail use layers were derived from traffic volume data collected from roads and trail surveys conducted by Parks Canada and Public Works within the study area (Table 2.5). Road layers were reclassified to low human use density (0 – 1,000 automobiles per day) and high use density (> 1,000 automobiles per day). Trail layers were reclassified to low human use density (0 – 100 users per month) and high human use density (>100 users per month). Using the digital road and trail data, I developed a distance to roads and trails layer for each category of use, as the Euclidean distance from the road or trail. Distance to roads is a more appropriate measure of road and trail effects than density of roads and trails because in mountainous topography road placement is cheapest in the valley bottoms, resulting in low road density throughout the Central Rockies region. A distance to water layer was derived from a hydrological layer, as the Euclidean distance to the closest stream, river or lake.

Table 2.1. Total biomass of 649 prey animals killed or scavenged by wolves in the Central Rockies between 1987 – 1997. Biomass estimates weighted according to mean mass of species, age, and sex of identified kills as per Weaver (1994).

Prey Species	Total Biomass (kg)	Proportion in Winter Wolf Diet
Elk	87,477	0.706
Deer	9,972	0.080
Moose	23,664	0.191
Big Horn Sheep	2,504	0.020
Mountain Goat	361	0.003

Table 2.2. Equation used to derive prey layer. Numbers in parentheses indicate proportion of each prey species in wolf winter diet.

Elk layer * (0.706) + Deer layer * (.08) + Moose layer * (0.191) + Sheep layer * (0.02) + Goat layer * (0.003)

Table 2.3. Reclassification of Landsat vegetation image used to derive hiding cover image

Landsat Image Vegetation Type	Class	Reclassified Image HIDE
Conifer Dominated	1	5
Shrubland	2	4
Deciduous Dominated	3	4
Grassland	4	3
Water	6	2
Ice/Snow	7	1
Rock/Bare Soil	8	1
Anthropogenic	9	0

Table 2.4. Reclassification of Landsat vegetation image used to derive snow-shedding image.

Landsat Image Vegetation Type	Class	Reclassified Snow Image	Snow-Shedding Capability
Conifer Dominated	1	3	High
Shrubland	2	2	Moderate
Deciduous Dominated	3	2	Moderate
Grassland	4	1	Low
Water	6	1	Low
Ice/Snow	7	1	Low
Rock/Bare Soil	8	1	Low
Anthropogenic	9	0	N/A

Table 2.5. Traffic volume classification used to derive road and trail layer.

Traffic Volume	Road Class	Trail Class
0 – 10	1	1
11 – 100	2	2
101 – 1,000	3	3
1,001 – 10,000	4	4
10,001 – 100,000	5	N/A
>100,000	6	N/A

Home Range Analyses

Radiotelemetry data for each pack were pooled from the three winters of data collection, and one radio location per day was selected at random as the sample to determine home range for each pack (White and Garrot 1990). The adaptive kernel method (95% isopleth; Worton 1989) was used to derive the home range polygons in the program Calhome (Kie et al. 1994). In mountainous environments, however, standard home range estimators such as the adaptive kernel method fail to describe accurately spatial habitat use by wildlife because much of the area is unusable high elevation rock and ice. Similarly, low elevation areas with steep slopes are unused. Therefore, I eliminated areas with elevation and slopes unused by wolves to provide a more accurate home range (Figure 2.3). Home range polygons were imported into GIS, and the portion of the home range occurring below the maximum used elevation and slope (Table 2.6) was used as an estimate of each pack's home range.

Spatial Analysis

Using GIS (Idrisi 2.0; Eastman 1995), I generated 20,000 points from the tracking lines of each pack to represent use data. Points were derived from the tracking lines using a stratified random routine in GIS. I also generated 20,000 random points from within each pack's home range for a random dataset. The resolution of each point was 30 m x 30 m. For the final models, I arbitrarily selected a random set of 1,200 use points and 1,200 random points from each pack's dataset. Data from the four packs were pooled to generate a regional model. The regional model dataset included 300 use and 300 random points from each of the four packs.

Table 2.6. Maximum elevation used by four wolf Packs in the Central Rocky Mountains between November and March, 1994 – 1997.

Pack	Maximum Elevation (m)	Maximum Slope (degrees)
Bow Valley	2451	61
Cascade	2427	66
Kootenay	2189	53
Yoho	2139	53

The following parameters were extracted in GIS for each point: elevation (ELEV), aspect (ASP), slope (SLP), terrain ruggedness (TRUG), prey habitat quality (PREY), hiding cover (HIDE), snow shedding (SNOW), distance from high use (RDHI) and low use (RDLO) roads, distance from high use (TRHI) and low use (TRLO) trails and distance from water (WATER).

Univariate Analyses

Because some variables typically drop out of final multivariate models, I conducted univariate analyses to investigate the relationship between used and random points for each habitat variable and for each pack.

Model Building

I first developed a Spearman rank correlation matrix to assess the potential predictor variables for significance and to determine whether multicollinearity existed among predictor variables. I eliminated variables that were not significantly correlated with habitat use by wolves. I also eliminated the least explanatory of each pair of highly correlated (>0.70) variables because inclusion of highly correlated independent variables can lead to erroneous model results (Tabachnick and Fidell 1996). I then examined the importance of the potential predictor variables in explaining wolf habitat use with logistic regression (Manly et al. 1993). The logistic regression model probit equation is written as:

$$\text{Prob (event)} = 1/(1+e^{-Z}),$$

$$\text{where } Z=B_0 + B_1X_1 + B_2X_2 + B_pX_p$$

e is the base of the natural logarithm (~2.718),

B_0 - B_p are coefficients estimated from the data

X_1 - X_p are the independent variables (Norusis 1990)

The logistic regression coefficients indicate the contribution of each predictor variable to explaining wolf habitat. The sign (positive or negative) and strength (P value) of each predictor variable's coefficient represented the role of the predictor variable in explaining wolf habitat use. A positive sign for all variable coefficients except distance to roads, trails, and water implied attraction, whereas a negative sign indicated repulsion. A positive sign for distance to roads, trails, and water indicated repulsion, whereas a negative sign indicated attraction. Stepwise model fitting in logistic regression (SPSS 7.0, Norusis 1990) was used to generate a series of candidate models with good fit to the data. Parameters that were not statistically significant in the logistic regression were eliminated from the models. Alternate models were compared using Akaike's Information Criterion (AIC), a model-selection statistic that applies the principle of parsimony through balancing bias inherent in under-fitted models and higher sampling variance inherent in over-fitted models (Burnham and Anderson 1998). I also used classification accuracy of the response variable (use/random) to assess the models (Manly et al. 1993)

I generated a probability surface layer from the best approximating model for each pack and for the regional model using the probit equation. The probability surface shows the likelihood of occurrence of wolves in each 30 m x 30 m pixel within the study area.

Model Predictability

A dataset of 300 points derived from a portion of the snow tracking data not used to develop the models was used to validate each pack model, and a pooled dataset of 1200 points was used to validate the regional model. The points were overlaid on the probability surface and classified according to percent of points within high probability (>50%) and low probability (<=50%) areas. I also used a chi square analysis to test how well the models predicting probability of use corresponded to actual use by wolves of that landscape. I determined the proportion of each pack's home range that occurred within areas predicted to have a high (>50%) probability and a low (<=50%) probability of use. These proportions were used to derive the expected use by each wolf pack. The reserved data was then overlaid on the high/low probability map to determine the observed values. I used similar methods to test the predictability of the regional map, using the combined dataset of wolf locations to determine observed values.

RESULTS

Home Ranges

Winter home ranges were 1,651 km^2 for the Bow Valley pack, 595 km^2 for the Cascade pack, 1,490 km^2 for the Kootenay pack, and 448 km^2 for the Yoho pack (Figure 2.1). The regional study area was comprised of the four home ranges, a total of 4,185 km^2.

Univariate Analyses

None of the habitat data for the four wolf packs was deemed normally distributed based on the Lilliefors test (Norisus 1990), and could not be normalized through transformations. Consequently, the nonparametric Kruskal-Wallis test was used to investigate the relationship between used and random points (Table 2.8). The transformed continuous aspect data was used in the Kruskal-Wallis test, and circular statistics (Zar 1996) were used to determine mean aspect for used and random points (Table 2.7).

Univariate analyses show significant differences between used and random points for most habitat variables investigated, although some of the relationships with habitat variables varied among packs. Wolves in all four packs used significantly lower elevations and slopes, less rugged habitat, higher quality prey habitat, and habitat closer to trails and high use roads than expected based on availability within their home range (Table 2.8). Wolves in two of the four packs used aspect significantly different than expected (Table 2.8). Wolves in three of the four packs used vegetation with significantly higher hiding cover and snow shedding potential and used habitat closer to water and low use roads than expected (Table 2.8).

Logistic Regression

The logistic model for the Bow pack was highly significant (-2 log likelihood (LL) = 1876.9, $X^2 = 1450.3$, df = 4, $P < 0.0001$). Habitat variables retained in the model included elevation, prey habitat, low use trails and high use trails. All variables made significant contributions to the model. The model correctly classified 89% of used sites and 76% of random sites.

The Bow pack's movements were most strongly associated with elevation. The coefficient for elevation was negative, indicating a preference for areas of low elevation. The pack's movements were positively associated with areas of high prey habitat quality. The pack was negatively associated with distance to low and high use trails, indicating a preference for habitat closer to trails. The pack's movements were least influenced by low use trails (Table 2.9). Figure 2.3 shows the habitat use probability surface generated from the Bow Valley pack model.

The logistic model for the Cascade pack was highly significant (-2LL = 2424.7, X^2 = 902.4, df = 10, P < 0.0001). The model was comprised of elevation, prey habitat, hiding cover, high use trails, low use trails, and distance to water. All variables selected for the model made significant contributions. The model correctly classified 85% of used sites and 68 % of random sites.

The movements of the Cascade pack were most strongly associated with elevation, and the negative sign of the coefficient indicates a preference for lower elevations. The pack was positively associated with habitat near water, high prey habitat quality, and hiding cover. The pack was attracted to low and high use trails, and the pack's movements were least influenced by low use trails (Table 2.9). Figure 2.3 shows the habitat use probability surface generated from the Cascade pack model.

The logistic model for the Kootenay pack was highly significant (-2LL = 2327.4, X^2 = 999.7, df = 4, P < 0.0001). The model was comprised of elevation, low use roads, low use

Table 2.7. Comparison between mean used and random points by wolves for aspect (degrees), determined by circular statistics.

Pack	Aspect Used (degrees)	Aspect Random (degrees)
Bow	176	148
Cascade	145	136
Kootenay	174	180
Yoho	36	27

Table 2.8. Comparison between used and random points by wolves for habitat variables, determined by Kruskal-Wallis test.

	Bow Pack			Cascade Pack			Kootenay Pack			Yoho Pack		
Variable	Mean Used	Mean Random	P	Mean Used	Mean Random	P	Mean Used	Mean Random	P	Mean Used	Mean Random	P
ELEV	1506	1920	<0.001	1541	1843	<0.001	1237	1502	<0.001	1257	1542	<0.001
SLP	6.59	19.28	<0.001	7.65	19.62	<0.001	5.53	16.40	<0.001	9.43	20.95	<0.001
ASP	1.16	1.0	0.013	1.74	1.73	<0.001	0.90	0.93	0.097	1.03	1.06	<0.001
PREY	2.33	1.54	<0.001	2.41	1.9	<0.001	2.24	1.83	<0.001	1.97	1.67	<0.001
TRUG	1.07	2.42	<0.001	1.14	2.43	<0.001	0.86	1.99	<0.001	1.30	2.42	<0.001
HIDE	4.52	3.73	<0.001	4.22	3.61	<0.001	4.33	4.34	0.110	4.36	4.19	0.002
SNOW	2.56	2.14	<0.001	2.35	2.08	<0.001	2.40	2.43	0.095	2.47	2.34	0.001
RDLO	1853	5321	<0.001	5094	7098	<0.001	7947	6895	<0.001	1813	2750	<0.001
RDHI	1708	4106	<0.001	4814	7048	<0.001	1544	2662	<0.001	2352	3124	<0.001
TRLO	483	1249	<0.001	690	1252	<0.001	884	1759	<0.001	571	1737	<0.001
TRHI	1852	3320	<0.001	2336	4424	<0.001	[a]	[a]	[a]	11549	12719	<0.001
WATER	269	437	<0.001	261	370	<0.001	163	235	<0.001	176	216	<0.001

[a] no high use trails in home range

Table 2.9. Variables in logistic regression models for four wolf packs and a regional model, showing coefficients, standard errors, and significance values.

Pack	Variable	Coefficient	Standard Error	P
Bow	CONSTANT	11.8373	0.6656	<0.0001
	ELEV	-0.0072	0.0004	<0.0001
	PREY	0.2829	0.0725	0.0001
	TRLO	-0.0003	7.70E-05	0.0004
	TRHI	-0.0002	2.67E-05	<0.0001
Cascade	CONSTANT	5.1904	0.5163	<0.0001
	ELEV	-0.0030	0.0003	<0.0001
	PREY	0.2948	0.0731	0.0001
	TRLO	0.0002	6.51E-05	0.0038
	TRHI	-0.0002	2.04E-05	<0.0001
	DISWATER	-0.0007	0.0002	0.0011
	HIDE			<0.0001
	HIDE1	-0.9275	0.5887	0.1151
	HIDE2	-0.3267	0.2358	0.1659
	HIDE3	1.1726	0.2609	<0.0001
	HIDE4	-0.3800	0.2335	0.1037
	HIDE5	0.3746	0.1620	0.0208
Kootenay	CONSTANT	9.9883	0.5883	<0.0001
	ELEV	-0.0079	0.0005	<0.0001
	TRLO	-0.0003	4.589E-05	<0.0001
	RDLO	0.0001	1.579E-05	<0.0001
	DISWATER	-0.0014	0.0003	<0.0001

Yoho	CONSTANT	6.0095	0.3361	<0.0001
	ELEV	-0.0036	0.0003	<0.0001
	TRLO	-0.0013	8.15E-05	<0.0001
	DISWATER	0.0009	0.0003	0.0013
Regional	CONSTANT	8.2119	0.6314	<0.0001
	ELEV	-0.0048	0.0004	<0.0001
	PREY	0.2014	0.0709	0.0045
	TRLO	-0.0004	8.04E-05	<0.0001
	TRHI	-9.1E-05	1.085E-05	<0.0001
	RDHI	7.91E-05	1.59E-05	<0.0001
	TRUG	-0.3420	0.0680	<0.0001

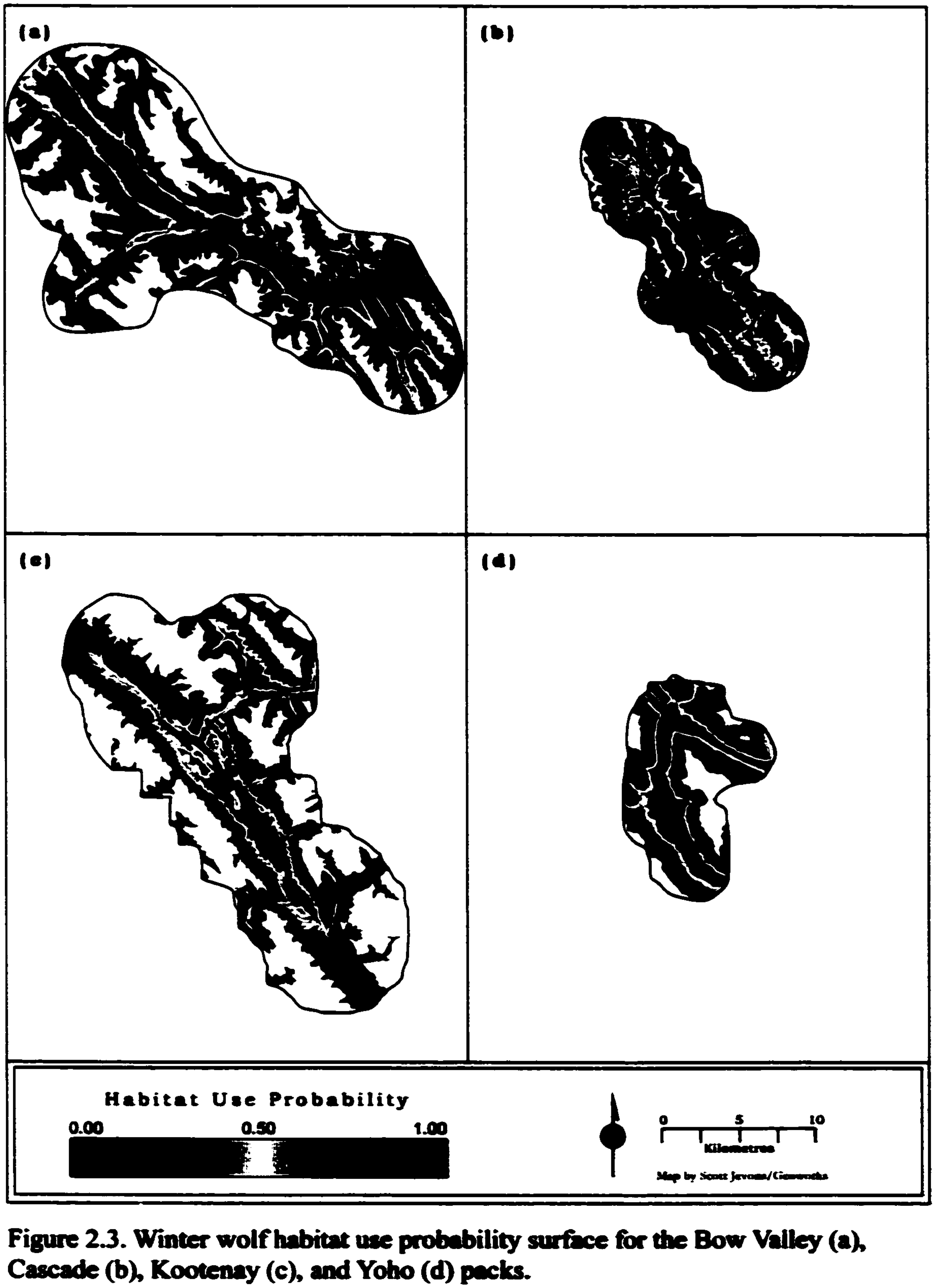

Figure 2.3. Winter wolf habitat use probability surface for the Bow Valley (a), Cascade (b), Kootenay (c), and Yoho (d) packs.

trails and distance to water. All variables made significant contributions. The model correctly classified 86% of used sites and 66 % of random sites.

The movements of the Kootenay pack were most strongly associated with elevation, and the negative sign of the coefficient indicates a preference for lower elevations. The pack was positively associated with distance to low use roads, indicating an avoidance of low use roads or of habitat adjacent to these roads. The pack was negatively associated with distance to low use trails, indicating a preference for using the trails or habitat closer to trails. The pack was negatively associated with distance to water, indicating a preference to travel through habitat near water. Distance to water had the least influence on the pack's movements (Table 2.9). Figure 2.3 shows the habitat use probability surface generated from the Kootenay pack model.

The logistic model for the Yoho pack was highly significant (-2LL = 2251.1, X^2 = 1076.1, df = 3, P < 0.0001). The model was comprised of elevation, distance to water, and low use trails. All variables made significant contributions. The model correctly classified 83% of used sites and 70 % of random sites.

The movements of the Yoho pack were most strongly associated with low use trails, and the negative sign of the coefficient indicates a preference for using trails or habitat closer to trails. The pack was negatively associated with elevation, indicating a preference for lower elevations. The pack was positively associated with distance to water, indicating a preference for habitat farther away from water. The pack's movements were least influenced by distance to water (Table 2.9). Figure 2.3 shows the habitat use probability surface generated from the Yoho pack model.

The regional model was also highly significant (-2LL = 1663.8, $X^2 = 831.6$, df = 6, P < 0.0001). The model was comprised of elevation, prey habitat, high use roads, high use trails, low use trails, and terrain ruggedness. All variables made a significant contribution. The model correctly classified 86% of used sites and 71% of random sites.

Data from the four packs in the regional model were most strongly associated with elevation, and the negative sign of the coefficient indicates a preference for lower elevations. The movements of the wolves were positively associated with prey habitat, indicating a preference for high quality prey habitat, and positively associated with high use roads, indicating an avoidance of these roads or of habitat closer to high use roads. The packs' movements were negatively associated with low and high use trails, indicating a preference for using the trails or habitat close to the trails. The wolves were negatively associated with terrain ruggedness, indicating an avoidance of highly variable habitat. The movements of the wolves were least influenced by prey habitat quality (Table 2.9). Figure 2.4 shows the habitat use probability surfaced generated from the regional model.

Model Predictability

The binary classification accuracy of the models was high for all models. The majority of snow-tracking sample points for each pack (80 – 86%) and for the regional model (93%)

occurred within areas predicting high probability (>50%) of wolf use (Table 2.10).

Chi square tests of how well the models corresponded with actual use of wolves on the landscape were all significant (Table 2.11). Wolves in all packs and at the regional level used their home range out of proportion to the availability of areas classified as habitat with low and high probability of wolf use.

Figure 2.4. Winter wolf habitat use probability surface for the Central Rocky Mountain region.

Table 2.10. Validation classification results for logistic regression models of four wolf packs in the Central Rocky Mountains

Pack	Points in Areas of High Probability (%)	Points in Areas of Low Probability (%)
Bow	86	14
Cascade	80	20
Kootenay	86	14
Yoho	84	16
Region	93	7

Table 2.11. Chi square tests of use by wolves of areas classified by logistic regression models as low and high probability of use. Expected values derived from proportion of home range that occurs in low (<50% probability of use) or high (>50% probability of use) probability areas

Pack	Observed Low Probability	Expected Low Probability	Observed High Probability	Expected High Probability	X^2	P
Bow	42	243	258	57	270.0	<0.0001
Cascade	60	213	240	87	157.3	<0.0001
Kootenay	42	264	258	36	328.7	<0.0001
Yoho	48	213	252	87	184.6	<0.0001
Region	21	189	279	111	206.8	<0.0001

DISCUSSION

The probability that a wolf will use a certain habitat may be a function of its behavioural response to a gestalt of factors, including the physical environment, distribution of prey, and interspecific and intraspecific interactions. The ultimate mechanisms of habitat selection may be difficult, however, to decipher. Both evolutionary and behavioural factors govern habitat use decisions. Habitat selection is a product of evolutionary factors conferring survival and fitness values to the habitat selection process, and of behavioural responses providing the proximate elements of habitat selection (Krebs 1978). Although it may be impossible to determine the precise habitat stimuli that animals respond to, this does not preclude the construction of a model that predicts habitat use with a relatively high degree of accuracy. The primary cue that wolves respond to may be prey abundance and distribution, for example, but elevation appears to be a better predictor of wolf habitat use. Although elevation is not likely a cue that wolves perceive, it influences vegetation and climatic regimes to which wolves and their prey respond.

Social animals such as wolves likely develop traditions of habitat use. There is evidence that among long-lived species, knowledge of travel routes is passed down by tradition from generation to generation (Mech 1970; Curatolo and Murphy 1986; Thurber et al. 1994; S. Herrero pers. comm.). Intensive radiotelemetry monitoring, and tracks and scats, indicate that wolves use the same trails in our study area year round (Paquet and Callaghan unpublished data). A newly colonizing wolf pack may respond to one set of habitat cues while first establishing their travel routes, and another set of cues subsequently while using the established travel routes.

The best predictors in my models of wolf habitat use were topographical, vegetation, and anthropogenic variables. Although the combinations of predictors varied among wolf packs, the strongest variable for three of the four pack models and for the regional model was elevation. Elevation influences climate, and the combined effects of elevation and snow depth concentrate the activities of wolves and their primary prey into forested valley bottoms and relatively low slopes (Huggard 1993a; Paquet 1993; Paquet et al. 1996). Elevation was also a predictor of wolf habitat use in other research in the Rocky Mountains (Singleton 1995; Alexander et al. 1996; Paquet et al. 1996; Boyd-Heger 1997). The long-distance travel routes of wolf packs that I recorded typically link montane river valleys via low elevation mountain passes (Figure2.4). The extent of rugged mountain topography in the Central Rockies severely limits the availability of landscape linkages and, consequently, the amount of wolf habitat is far less than the areal extent of the landscape (Paquet et al. 1996). In contrast, habitat available to wolf packs occupying homogeneous terrain actually increases during winter months because frozen lakes and rivers provide alternate travel routes. Thus, although the wolf is considered to be a habitat generalist (Mech 1970; Fuller et al. 1992; Mladinoff et al. 1995), my models indicate that biophysical features in mountainous terrain strongly influence their movements during winter.

Other predictor variables in the logistic models include high and low use trails, prey habitat, hiding cover, distance to water, high use and low use roads, and terrain ruggedness. Wolf packs tended to use higher prey habitat quality, which is consistent with other research that suggests wolf movements maximize prey encounters (Huggard 1993a; Huggard1993b). Wolves were attracted to low use and high use trails, and to habitat that was relatively less rugged. Wolf packs also tended to travel through vegetation that provided greater hiding cover capability, such as closed coniferous forest. Formozov (1946) suggested that deep snow make portions of habitat unusable for wolves due to morphological limitations, and that snow conditions influence wolf use of habitat by affecting prey availability. Corsi et al. (1999) found that dense forest cover was positively correlated with wolf presence.

The univariate analyses provided a summary of wolf habitat use patterns in winter. With few exceptions, wolves tended to use areas of lower elevations and slopes, less rugged terrain, and tended to travel through vegetation providing adequate hiding cover and snow-shedding capability that was closer to water, roads and trails. Elevation may be an "umbrella" habitat variable, in that low elevation valley bottoms tend to have lower slopes, less rugged terrain, denser vegetation, and are close to water. The majority of roads and trails also tend to be constructed through low elevation valley bottoms.

The list of predictor variables for the logistic regression models varied among packs, indicating that different habitat relationships may exist among the various territories. This variation among packs may give insights into local habitat relationships, and should not be considered systemic noise (Morrison et al. 1998). The variability in elevation, slope and terrain ruggedness is high throughout the study area, and wolves likely respond to local conditions. Moreover, the orientations of the main valleys differ among pack home ranges, which likely influences the vegetative regimes that prey populations and in turn, wolves, respond to. Other factors, such as competition and stochastic events, may affect habitat use differentially at the pack level.

Predictor variables also vary between the regional and pack models, indicating that my models are scale sensitive. The best utility of regional-scale models may be to identify factors associated with species' distribution. They may not, however, reflect the habitat variability extant among local populations as a consequence of averaging (Morrison et al. 1998). Therefore regional-scale models may not be a sufficient stand-alone tool for detailed conservation plans (Carroll et al. 2000).

My results suggest that wolves are attracted to roads and trails during winter. Human activities that modify snow compaction, including cross-country skiing, snowmobiling, and ploughing roads, may influence winter movements of wolves by providing efficient travel routes (Paquet et al. in review). The chest height of wolves (approximately 40 cm) causes limitations while moving in snow deeper than 40-50 cm (Kelsall 1969; Mech 1970; Pulliainen 1982). Travelling along human-modified trails might confer energetic benefits to wolves even where snow conditions do not exceed the morphological threshold.

I found that wolves used habitat with deep snow conditions only while traveling on ploughed roads or track-set trails, and wolves travelling along natural trails tended to use vegetation with high snow-shedding capability. Moreover, use of elevation differed significantly on human-modified trails and natural trails (Paquet et al. in review). Other studies have shown similar attractions of wolves to compacted roads and trails during winter (Formozov 1946; Green 1951; Mech 1970; Zalozny 1980; Bjarvell and Isakson 1982; Paquet 1993). The influence of human activity on winter wolf movements may alter wolf-prey relations by allowing wolves more efficient access to prey (Paquet et al. in review). GPS collared wolves in Central Alberta travelled faster on compacted linear features than in the forest (James 1999) and caribou kills were closer to linear features than expected by chance (James and Stuart-Smith 2000). Similarly, wolves in Poland travelled faster on compacted linear features and frozen rivers than in the forest (Musiani et al. 1998).

Research in relatively homogeneous terrain identified road density as a good predictor of wolf habitat use, whereby pack territories were located in areas with lower road densities than in random non-pack territories (Mladinoff et al. 1995; Mladinoff et al. 1999). Road density is not, however, an adequate predictor of wolf habitat use in mountainous terrain due to the effects of topography. Because placement of roads is cheaper in valley bottoms, road density is relatively low throughout the most rugged habitat within the Central Rockies.

Human developments, in the form of roads, trails and facilities, and the level of human activity, have increased in the Central Rockies over the past decade (Paquet et al. 1996). Topographical and climatic factors restrict wolf movements to low elevation areas during the winter, and anthropogenic factors allow wolves to move more efficiently through the landscape as well as restrict movements through areas of high human activity. The placement of roads in areas of high winter wolf activity does not deter wolves from using habitat near roads but increases the probability of wolf mortality from automobile collisions and exposure of wolves to human hunters in non-protected areas. The convergence of wolf and human activities during the winter may have either positive or negative effects on wolves. On a regional scale, much of the low elevation wintering habitat for prey species exists outside of the protected areas. Because wolves naturally follow prey movements outside of the protected areas, conservation of wide ranging carnivores such as wolves may require interjurisdictional cooperation of the managing agencies. This study was not designed to assess the influence of habitat parameters on population density or reproductive success (Van Horne 1983), but developing predictive habitat use models is an important step in the process of determining the effects of anthropogenic-induced and natural trends in habitat change on population persistence.

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CHAPTER THREE

SURVIVAL OF WOLVES IN THE CENTRAL ROCKY MOUNTAINS OF CANADA

INTRODUCTION

Estimating survival rates is an important part of measuring viability of populations. Management of protected wolf populations requires quantitative measurements of demographic parameters such as survival rates to identify factors that drive population change. In mountainous areas, however, estimates of survival rates are difficult to obtain for wolves owing to low densities and wide-ranging movements.

Although wolves are endemic to the Central Rocky Mountains (Green 1951), the population was severely reduced between 1952 and 1956 through a predator culling program that occurred within and outside of protected areas in the region (Ballantyne 1956; Gunson 1992). Wolves naturally recolonized the Central Rockies between the early 1970s and early 1990s (Paquet 1993). Survival may be higher during early years of a recovering population due to lower intraspecific competition and higher prey density (Hayes and Harestad 2000).

In the Central Rocky Mountains, steep, rugged terrain dominates the landscape. The topographical and climatic effects of mountainous terrain confine wolf movements to low and mid elevations and result in wolf packs maintaining large home ranges. Roads occur at low elevations that are also preferred by wolves (Chapter 2), providing access to hunters and trappers. Moreover, habitat availability is reduced during the winter due to snow depths at higher elevations. During the fall and winter, wolves spend more time near wintering grounds of elk (*Cervus elaphus*), their primary prey. Such wintering grounds exist in low elevations areas that typically border the protected areas in the region, such as the east slopes of the Rocky Mountains adjacent to Banff National Park. These movements coincide spatially and temporally with activities of hunters and trappers (J. Jorgenson Alberta Department of Sustainable Resource Development, pers. comm.). Roads may therefore have an inordinate effect on wolf survival in mountainous areas.

Demographic studies of wolves have focused on differences in survival rates with respect to single factors (e.g. males versus females or adults versus juveniles) rather than on interacting effects of independent variables (Fuller 1989; Ballard et al. 1987; Pletscher et al. 1997; Hayes and Harestad 2000). Herein, I use a multivariate approach to investigate how human activities and roads interact to influence survival of wolves in a matrix of protected and unprotected areas.

I investigated survival rates and causes of mortality for radiocollared wolves from 12 packs in the Central Rocky Mountains. Of the 12 packs, 9 territories spanned protected and non-protected areas, 1 territory occupied a protected area exclusively, and 2 territories occurred in a non-protected area. I used mortality data to (1) document causes of mortality, (2) estimate average seasonal survival (S_s), (3) estimate average annual survival (S_a), and (4) assess the relative effects of eight variables (age, sex, season, region, hunting activity, trapping activity, roads and traffic volume) on S_s. Specifically, I tested whether (1) wolf survival was lower in smaller protected areas than in larger protected areas; (2) survival was higher for wolves occupying protected areas than for those whose territories spanned protected and non-protected areas; (3) roads in the core of a wolf pack territory reduced survival due to increased potential for collisions with automobiles and increased hunter/trapper access; (4) traffic volume affected survival; (5) survival of pups was lower than adults; and (6) wolf survival was higher during the early years of population recovery than during later years.

STUDY AREA

This study was conducted in portions of Banff National Park, Alberta, Kootenay and Yoho National Parks, British Columbia, Kananaskis Country Recreation Area, Alberta, and portions of provincial land extending beyond protected areas between 30 April 1987 and 31 December 2000 (Figure 3.1). The study was initiated in the Bow River Valley following the colonization of the valley by two wolf packs. As the population increased, the study area expanded eventually to cover 18,670 km^2 of the Central Rocky Mountains. The area consists of national and provincial parks where wolves are protected from hunting and trapping and non-protected provincial parks, crown land, and private land.

Topographic and vegetative features are described in Chapter 2. Small towns, roads, developments, and timber harvest are scattered throughout the study area (Figure 3.1). Transportation routes in the study area consist of two major transcontinental transportation routes, several secondary highways, and numerous access roads, rural, and forestry roads, which are described in Chapter 2.

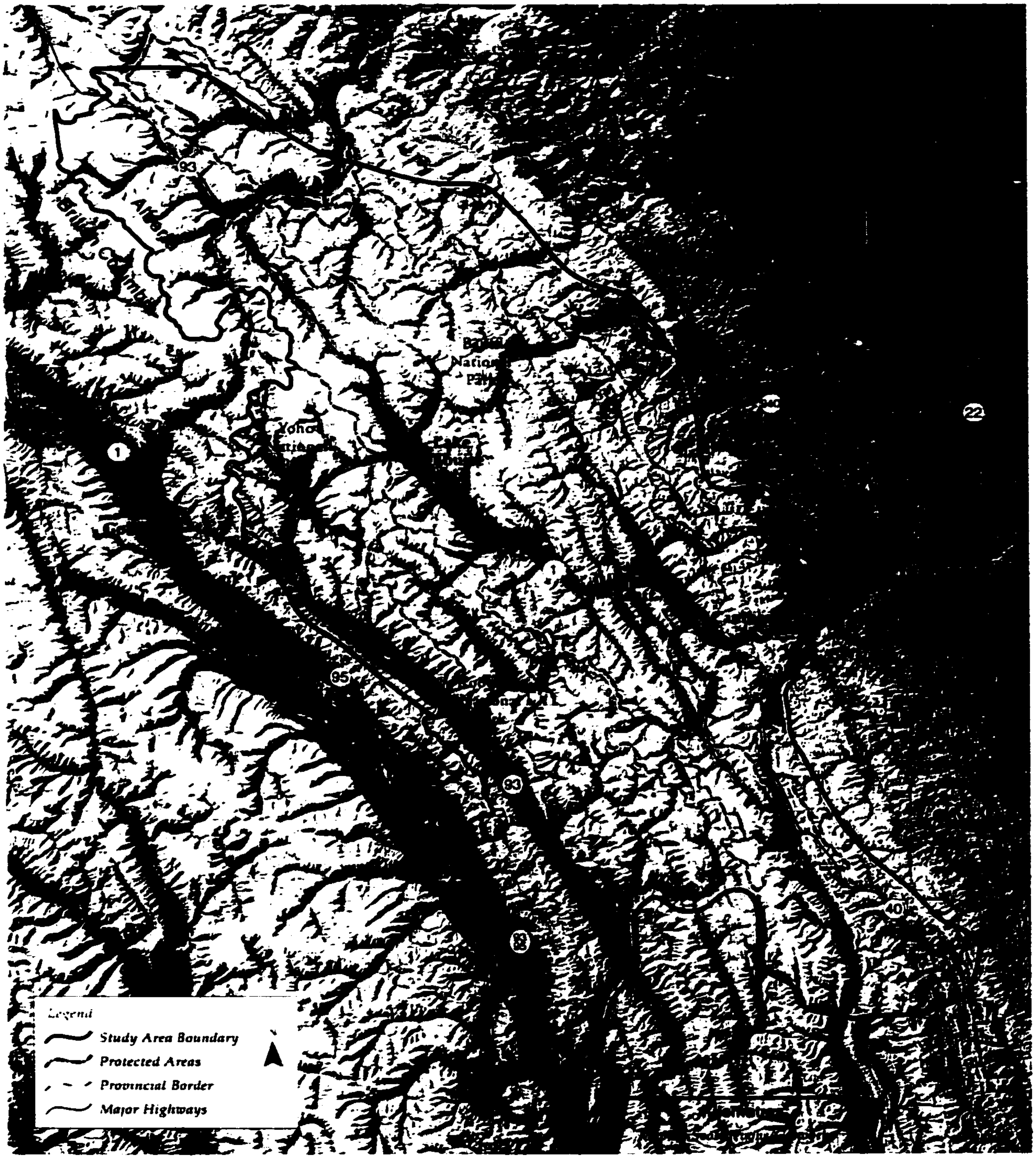

Figure 3.1. Study area in 18,700 km^2 of the Central Rocky Mountains, Canada.

Average daily traffic volume during the study period was 7,743 automobiles on the TCH (Redearth Creek Counter), 2,724 automobiles on Hwy 93 (Storm Mountain Counter), 782 automobiles on Hwy 1A (BVP East Monitor, Public Works Canada unpublished data), and 1,901 automobiles on Highway 40 (Barrier Lake Monitor, Alberta government unpublished data). Traffic volume data were not collected for the rural and forestry roads in the study area, although traffic volume on these roads was likely much lower than on the highways (S. Donelon, AB Department of Community Development; B. Forbes, B.C. Ministry of Environment, pers. comm.).

Four relatively large protected areas occur within the study area: Banff, Kootenay, and Yoho National Parks, and Peter Lougheed Provincial Park. Several smaller protected areas also exist within the study area. Hunting or trapping wolves is not permitted within these protected areas. The Provinces of Alberta and British Columbia regulate wolf hunting and trapping elsewhere in the study area. On crown and private land in Alberta, wolf hunting by residents is permitted 9 months per year without a bag limit. Landowners or grazing leaseholders on crown land are permitted to hunt wolves 12 months a year without a bag limit. Numerous trap lines exist adjacent to Banff National Park and several exist within Kananaskis Country. Trappers are permitted to kill wolves between October 31 and February 28 without a bag limit (Alberta Environment 2000). In the Kootenay District of British Columbia, wolf hunting by residents is permitted 9 months per year without a bag limit in areas below 1100 m and with a bag limit of 2 wolves per year in areas above 1100 m. Trappers are permitted to kill wolves 12 mos. a year in the East Kootenay trench in areas below 1100 m, and between October 15 and February 15 in areas above 1100 m (British Columbia Ministry of Environment, Lands and Parks 2000). A few trap lines exist adjacent to Kootenay and Yoho National Parks.

METHODS

Forty-two wolves from 13 packs were captured, radiocollared, and monitored between 1987 and 2000 (Figure 3.1). Capture and immobilization methods are described in Chapter 2 and in Paquet (1993). VHF or satellite radiocollars (LOTEK Engineering, Newmarket, ON) were fitted on the wolves before release. Attempts were made to relocate collared animals daily via ground telemetry or weekly or bi-weekly via aerial telemetry (fixed wing or helicopter) following Mech (1983). Radiocollars were sensitive to movement and changed pulse rate after approximately four hours of inactivity after a radiocollar was shed or the animal had died.

Upon detecting a mortality signal, usually within one week of death, attempts were made to determine cause of death. Wolf deaths were classified as highway, railway, shooting, trapping, natural accidents, human-caused accident, and unknown. A death caused by a prescribed burn was categorized as a human-caused accidental death. If date of death was unknown and severe decomposition had occurred, death was classified as unknown and a death date was assigned at the midpoint between the last date of radio relocation and the date when death was confirmed. Carcasses recovered intact were necropsied by a wildlife veterinarian in Banff National Park or in an Alberta Department of Agriculture necropsy facility in Airdrie, AB.

The complete dataset consisted of 42 wolves, 19 of which died, 4 of which were alive at the end of the study, and 19 of which were removed from the dataset before the end of the study (right censored) due to radio failure or emigration from the study area. The right censored component constituted 45% of the dataset and included 7 animals whose fates were known following radio-failure. A high proportion of right censored data can affect the accuracy of survival estimates (Kalbfleisch and Prentice 1980). I therefore removed all individuals whose fates were unknown (due to radio failure or leaving the study area) from the data set but included information on those animals whose fates were known despite radio failure (except for one wolf that dispersed beyond the Central Rockies to southeastern Montana). This truncated dataset consisted of 31 animals, 24 of which were dead and 7 of which were still alive and therefore censored at the end of the study period. Because the survival estimates did not differ significantly between the two groups ($X^2 = 0.068$, $P > 0.05$), I have more confidence in the survival estimate for the truncated dataset because a smaller proportion of animals (23%) were censored.

Statistical Analyses

The nonparametric Kaplan-Meier method (Kaplan and Meier 1958) and staggered entry design (Pollock et al. 1989) were used to estimate seasonal and annual survival in the program SPSS 7.0 (Norusis 1990). Data were pooled into seasonal (spring, summer, fall, and winter) and yearly (May 1 – April 30) intervals, and wolves that were radiocollared in one time interval and survived to the next interval were removed from the dataset (right censored) on the last day of the interval and reintroduced as new independent observations on the first day of the following interval. I assumed wolves were randomly sampled, that survival times for individuals were independent, and that trapping, handling, and radiocollaring did not affect survival probability (Pollock et al. 1989, White and Garrott 1990). Because individual wolves were radiocollared at different times throughout the study (staggered entry design), I assumed that each radiocollared wolf introduced to the dataset (left-censored) had survival distributions similar to previously marked animals. I compared survival rates between groups using log rank X^2 tests (Pollock et al. 1989).

Poisson regression (Statistix 7.0 Analytical Software; Selvin 1995) was used to compute maximum likelihood estimates for seasonal survival while assessing the effects of eight independent variables. Poisson regression is useful for investigating the effects of a set of independent variables on a dependent variable that is expressed as a rate (e.g. survival rate; Selvin 1995). A multivariate approach has advantages over a univariate approach because it investigates relationships among variables and avoids inconsistencies of univariate analysis (e.g. effects of study area) (Hanley and Parnes 1983). The poisson regression method relates a rate to a series of independent variables, uses individual animals as sample units, and does not assume normality of independent variables (Selvin 1995). The following independent categorical variables were modeled to test for interactive effects on the dependent variable survival: age, sex, season, region, hunting activity, trapping activity, roads, and traffic volume.

I modelled time in three-month intervals (December–February, March–May, June–August, September-November; referred to hereafter as seasons) and as a polytomous variable (Hosmer and Lemeshow 1989). A similar protocol was followed as in the Kaplan-Meier procedure to censor wolves that survived from one interval to the next. A risk variable was expressed as the number of deaths per 1,000 radiodays in each time interval.

Each wolf was assigned to one of four regions [Banff National Park, Alberta (BNP); Kananaskis Country, Alberta (KCTY); Kootenay National Park, British Columbia (KNP); and Yoho National Park, British Columbia (YNP)]. The regions of Banff, Kootenay, or Yoho National Parks also included adjacent provincial land. I assigned wolves to a region according to where the majority (>80%) of their radiotelemetry locations occurred. I also categorized wolves according to whether their territories existed wholly within protected areas or spanned protected and non-protected areas.

Wolves that were radiocollared as juveniles and survived to age two were censored at the end of the spring interval of their second year and reintroduced on the first day of the summer interval as adults. Binomial categories of 0 or 1 were assigned to the trapping and hunting variables in each time interval for each wolf according to whether hunting or trapping activity occurred within the wolf's territory. Similarly, binomial categories of 0 or 1 were assigned to the roads variable according to whether roads were present in the core of the wolf's territory. I modeled traffic volume as a polytomous variable to represent low, medium, or high traffic volume on roads within the wolf's territory.

Stepwise model fitting in poisson regression (Statistix 7.0) was used to generate a series of candidate models with good fit to the data. Parameters that were not statistically significant ($P>0.05$) in the poisson regression were eliminated from the models. Alternate models were compared and the most parsimonious model was selected using Akaike's Information Criterion (AIC), a model-selection statistic that applies the principle of parsimony through balancing bias inherent in under-fitted models and higher sampling variance inherent in over-fitted models (Burnham and Anderson 1998).

RESULTS

Most (n=17, or 55%) of the collared animals occupied territories in Banff National Park; 5 (16%) occupied a territory in Kootenay National Park; 4 (13%) occupied a territory in Yoho National Park; and 5 (16%) occupied territories in Kananaskis Country (Figure 3.1). Collared wolves were monitored over 56 seasons and individuals for 11.4 ± 1.8 (mean $\pm$ SE) seasons (range 1-38 seasons).

Most (n=24, 77%) of the collared sample occupied territories that bordered protected and non-protected areas. The remaining 7 collared wolves (23%) occupied territories that existed wholly within a protected area. Some wolves occupied both types of territories during the study. The Cascade pack's territory, for example, existed wholly within Banff National Park from the time the pack was colonized in 1991 until the winter of 1997/98, when they expanded their territory to include unprotected provincial land adjacent Banff National Park.

Mortality and Survival Rate Estimation

Twenty-four mortalities (77%) were recorded during the study. Cause of death included natural deaths (n=5, 21%), shooting (n=11, 46%), trapping (n=1, 4%), human-caused accident (n=1, 4%), automobile (n=3, 13%) or train collision (n=2, 8%), and unknown (n=1, 4%) (Table 3.1). Human-caused deaths constituted 75% of total mortalities. Natural accidents included deaths resulting from avalanche or injuries sustained during predation attempts. No wolves were known to have died of old age or disease, although three wolves died at age 10.

Most of the deaths occurred during the fall (n=11, 46%) and winter (n=7, 29%) (Table 3.1). A greater proportion of deaths resulting from shooting occurred in Kananaskis Country and Kootenay and Yoho National Parks than in Banff National Park (Table 3.2). Conversely, a greater proportion of deaths resulting from automobile and train collisions occurred in Banff National Park than in the other areas (Table 3.2).

Although 10 of 12 packs occupied protected areas, all but one pack were exposed to human-caused mortalities outside of the protected areas. Most (67%) of human-caused wolf mortalities occurred outside of reserves. Of these mortalities, 45% occurred within 5 km of a reserve border. One wolf was shot while travelling 20 km from his territory during an extra-territorial foray and two wolves were shot while dispersing from their natal pack.

Average seasonal survival (S_s) was 0.93 (SE=0.01; 95% C.I.=0.90 – 0.95) (Table 3.3). Average annual survival (S_a) was 0.77 (SE=0.05, 95% C.I.=0.64 – 0.83) (Table 3.4). Average annual survival rate for wolves occupying protected areas (0.89; SE=0.05) was significantly higher (t-test, equal variance not assumed, P=0.026) than for wolves whose territories bordered protected and non-protected areas (0.72; SE=0.05). There was no significant difference in seasonal survival rates ($X^2 = 0.16$, df=1, P=0.69) or in annual survival rates ($X^2 = 0.09$, df=1, P=0.76) between early years of population recovery (1987 – 1993) and later years (1994 – 2000). Of the wolves that died and whose social status was known, 73% (n=11) of alpha animals, 100% of subdominant animals (n=7), and 75% (n=4) of pups were killed by humans.

Factors Affecting Mortality and Survival

The most parsimonious poisson regression model that appeared to explain S_s retained all independent variables except traffic volume and trapping activity. The model was highly significant (-2log likelihood = 8169.87, df = 346, p < 0.0001). All remaining variables made significant contributions to the model (p<0.05, Table 3.5). Seasonal survival was most closely related to region. The coefficient for region was positive, indicating that Banff National Park had the highest relative survival rate, followed by Kananaskis Country and Yoho National Park. Kootenay National Park had the lowest relative survival value. Seasonal survival was positively associated with age, indicating that adults had a higher relative survival rate than pups. Seasonal survival was also positively associated with sex, indicating that females had a higher relative survival rate than males.

Table 3.1. Seasonal mortality by cause recorded for radiocollared wolves in the Central Rocky Mountains, 1987-2000.

Mortality Cause	Spring	Summer	Fall	Winter
Highway	_	_	1	2
Hunting	1	-	7	3
Trapping	-	-	-	1
Railway	-	2	-	1
Natural	2	-	3	-
Human-Caused Accident	1	-	-	-
Unknown	-	-	-	1
Totals	4	2	11	7
Total Radiodays	7590	8051	7990	7339

Table 3.2. Wolf mortalities by cause recorded for radiocollared wolves in four regions of the Central Rocky Mountains, 1987-2000.

Mortality Cause	BNP	KCTY	KNP	YNP
Highway	2	-	1	-
Hunting	2	3	3	3
Trapping	1	-	-	-
Railway	2	-	-	-
Natural	3	1	1	-
Human Caused Accident	1	-	-	-
Unknown	-	-	-	1
Total	11	4	5	4

Hunting activity and roads were negatively associated with wolf survival. Survival also varied with season (Table 3.5).

Table 3.3. Kaplan-Meier estimates of seasonal survival calculated from wolves of all ages that were radio collared in the Central Rocky Mountains in Canada between 1988 – 2000.

Season (pooled across years)	Total no. at risk (r_t)	No. right censored	No. or deaths (d_i)	Seasonal Survival[a] (S_t)	SE	95% interval on S_t	
						lower	upper
Spring	31	0	5	0.952	0.023	0.884	0.981
Summer	31	0	2	0.978	0.016	0.922	0.994
Fall	31	0	11	0.882	0.033	0.801	0.933
Winter	31	7	6	0.919	0.960	0.842	0.960
Cumulative Seasonal Survival Rate				0.932	0.013	0.901	0.954

[a] Staggered entry of new animals into the study following Pollock et al. (1989).

Table 3.4. Kaplan-Meier estimates of annual survival calculated from wolves of all ages that were radiocollared in the Central Rocky Mountains in Canada between 1988 – 2000.

Year	Total no. new radios applied	No. at risk (r_i)	No. of animals right censored	No. of deaths (d_i)	Survival[a] (S_t)	SE	95% interval on S_t lower	95% interval on S_t upper
1988	1	2	0	0	1.000			
1989	3	5	0	1	0.800	0.179	0.414	0.958
1990	0	4	0	2	0.500	0.250	0.188	0.812
1991	3	5	0	1	0.800	0.179	0.414	0.958
1992	3	7	0	1	0.857	0.132	0.514	0.971
1993	4	10	0	3	0.579	0.199	0.254	0.847
1994	3	10	0	2	0.800	0.127	0.508	0.939
1995	1	9	0	4	0.556	0.166	0.302	0.783
1996	4	9	0	0	1.000			
1997	2	11	0	3	0.682	0.154	0.384	0.880
1998	0	9	0	1	0.978	0.105	0.585	0.978
1999	3	11	0	2	0.808	0.123	0.515	0.944
2000	2	11	7	4	0.636	0.145	0.370	0.839
Cumulative annual survival rate					0.769	0.045	0.642	0.827

[a] Staggered entry of new animals into the study following Pollock et al. (1989).

Table 3.5. Poisson regression model of seasonal survival of radiocollared wolves in the Central Rocky Mountains, 1987-2000. Aikaike's Information Criterion (AIC) was used for model selection.

Predictor Variables	Coefficient	SE	Coefficent/SE	P
Constant	-6.748	0.256	-26.34	<0.0001
Region	0.977	0.024	41.04	<0.0001
Sex	2.045	0.060	34.12	<0.0001
Hunt	2.98	0.122	24.35	<0.0001
Season	-0.766	0.034	-22.32	<0.0001
Age	1.051	0.087	12.11	0.0110
Roaded	0.261	0.103	2.54	<0.0001

DISCUSSION

Human-caused deaths were the greatest source of mortality (75%) for wolves in the Central Rockies. Shooting is the major cause of death for wolves in the Central Rockies, whereas in the protected Bow River Valley of Banff National Park, causes such as highway and railway mortality predominate. My results corroborate numerous studies that report human-caused deaths as the major source of wolf mortality (Fuller and Keith 1980; Berg and Kuehn 1982; Boitani 1982; Carbyn 1982; Mendelssohn 1982; Peterson et al. 1984; Ballard et al. 1987; Fuller 1989; Mech 1989; Jedrzejewska et al. 1996; Pletscher at al. 1997; Smietana and Wajda 1997; Boyd and Pletscher 1999). Furthermore, the patterns in my data suggest that social status of wolves affects vulnerability to human-caused mortalities.

The annual survival rate for wolves in the Central Rockies (0.77) was lower than that reported for a wolf population in the Yukon (0.84) that was temporarily protected while recovering from a cull (Hayes and Harestad 2000) and higher than that reported for an exploited population (0.48) in Alaska (Ballard et al. 1987). The survival rate for wolves in my study area was also lower than for wolves in the Flathead region of Montana and British Columbia (0.80) (Pletscher et al. 1997). Although the Flathead wolf population shares a similar history of recolonization with wolves of the Central Rockies, wolves occupying the Montana portion of the Flathead region are protected by endangered species legislation (Pletscher et al. 1997).

The multivariate model indicated a lower survival rate for pups than adults and, although the number of pups in the sample is small, this result is consistent with other studies (Keith 1983; Fuller 1989; Pletscher et al. 1997; Hayes and Harestad 2000). The model also indicated a regional effect on survival. Wolves survived longer in Banff National Park (6,641 km^2) than in Yoho or Kootenay National Parks, which are significantly smaller reserves (1,310 km^2 and 1,406 km^2). The size of Banff National Park likely buffers wolves from outside influences by providing relatively more montane habitat and a greater prey base. Only one wolf pack lives in each of Kootenay and Yoho National Parks, and both packs spend a considerable amount of time outside of protected areas, resulting in increased exposure to hunters and trappers.

The effects of roads on wolves include unintentional mortality through collisions with automobiles and increased access to hunters and trappers. Evidence exists for an increase in wolf mortality following improved road access (Person et al. 1996) and greater human-related mortalities in areas where road density was higher (Fuller 1989; Mech 1989). A threshold road density may exist that provides enough road access for humans to limit wolf populations through hunting, trapping, or poaching (Thiel 1985; Jensen et al. 1986; Mech et al. 1988). Several studies reported an avoidance of roads by wolves or selection of territories with lower road densities (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Fuller 1989). Although road density in the mountains is typically low, topographical complexity in mountainous areas concentrates wolves and their prey in low elevations during the fall and winter, which overlaps spatially with road placement and temporally with hunting and trapping activity by humans. Wolves occupying mountainous areas may be reluctant to avoid using habitat near roads because such low elevation habitat provides the greatest ease of travel and the greatest concentrations of prey (Chapter 2). Although no relationship between traffic volume and wolf survival was detected, highway fencing along 47.4 km of the Trans Canada Highway in Banff National Park may have reduced wolf-automobile collisions, thus increasing wolf survival and confounding my ability to detect a relationship.

Topography influences the spatial distribution of wolves, and topographical restrictions in my study area likely encouraged wolves to use habitat next to the mountainous reserves that has less relief (Chapter 2). The annual survival rates for adult wolves in the Central Rockies was lower (0.77) than for adult wolves in Yellowstone National Park (0.85, D. Smith National Parks Service, unpublished data). Only one pack of 12, and 7 of 31 radiocollared wolves, however, were fully protected by a reserve in the Central Rockies. Wolves whose territories spanned protected and non-protected areas had reduced survival. In contrast, 9 of 10 packs were fully protected by Yellowstone National Park, which spans 8,903 km^2.

The ability of individuals to use habitat adjacent to reserves reduces the isolation of the reserve, and may therefore positively affect population viability by providing immigrants (Newmark 1995). Conflict with humans on unprotected land next to reserves, however, may reduce survival in populations inhabiting protected areas. Large carnivores in particular are most exposed to threats on reserve borders because they range widely and occupy large home ranges (Woodroffe and Ginsberg 1998, 2000). The mean home range size of wolves in the Central Rockies is 1,709 km^2 (Chapter 5), which is considerably larger than those reported for areas of relatively homogeneous forested topography such as Minnesota (116 km^2, Fuller 1989), northern Alberta (283 km^2, Fuller and Keith 1980), central Manitoba (568 km^2, Carbyn 1980), and Wood Buffalo National Park (1,250 km^2, Oosenbrug and Carbyn 1985). Mountainous terrain may therefore exaggerate edge effects for wolves because a greater proportion of the population is exposed to reserve borders.

Wolves are also exposed to human-caused mortality inside protected areas. Of the 6 packs in my study area that occupied territories bisected by highways and railway lines, 5 lost members to automobile or train collisions. The pack that did not suffer effects of transportation corridors has been extant in the study area for only 2 years, occupies a territory where the Trans Canada Highway is fenced, and readily uses wildlife underpasses.

Although my data suggest that human activity is an important element of wolf survival, high annual productivity and dispersal capabilities of wolves provide wolves with resiliency against modest levels of human disturbance (Weaver et al. 1996). Topographical and climatic restrictions imposed on wolves occupying mountainous terrain may, however, reduce their resiliency to anthropogenic factors. Spatial structure may thus be an important element in the analysis of population vulnerability (Gilpin 1987). With current hunting and trapping regimes and an increase in road access or hunting activity, the border areas of the mountain parks in the Central Rockies may become mortality sinks whereby mortality exceeds reproduction.

Wildlife managers whose goal is to reduce human-caused mortalities in wolves occupying protected areas should focus on reducing the edge effects of protected areas in the region by managing road access and hunting and trapping regulations. Because wolves in the Central Rockies live in low densities, occupy large home ranges, and are drawn to lower elevation areas outside of reserves, a coordinated approach to wolf persistence across multiple jurisdictions is prudent.

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CHAPTER 4

THE INFLUENCE OF LINEAR FEATURES ON WOLF MOVEMENTS IN THE CENTRAL ROCKY MOUNTAINS

INTRODUCTION

There has been considerable interest in the effects of human disturbance on wildlife (Schultz and Bailey 1978; Curalto and Murphy 1986; Mumme et al. 1999; Schneider and Wasel 2000; Wilkie et al. 2000), and displacement of wildlife from habitat is one of the contemporary concerns (Gill et al. 1996). If wildlife respond to human disturbance by avoiding areas, the effect is equivalent to habitat loss or degradation (Gill and Sutherland 2000). Understanding the response of wildlife to anthropogenic change allows for predicting the consequences of such change (Pettifor et al. 2000).

Human-caused modifications of the landscape may change the spatial structure of the environment to which wildlife must respond. For example, human-constructed linear features such as roads, railway lines, trails, and power lines, may affect the spatial structure of wildlife habitat. Such modifications of the landscape can affect wildlife movements, population distribution, survival, and predator-prey dynamics (Bakowski and Kozakiewicz 1988; Brody and Pelton 1989; Mader et al. 1990; Paquet and Callaghan 1996; Jalkotzy et al. 1997; James and Stuart-Smith 2000). Natural linear features, such as rivers, may also influence wildlife movement patterns (Fuller and Robinson 1982). Although the effects of linear features on wildlife have been reported to be primarily negative, positive benefits of altered landscapes may accrue to some species (Mader et al. 1990; James and Stuart-Smith 2000; Paquet et al. in review).

Several studies have investigated the relationship between wolf movements or wolf population colonization and roads (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Thurber et al. 1994; Shelley and Anderson 1995; Mladenoff et al. 1995) but few studies have investigated fine scale responses of wolves to linear features (but see James and Stuart-Smith 2000). Using snow tracking to record the actual movement pathways of individuals is one method that allows for the testing of hypotheses about the environmental cues that affect movement, including repulsion or attraction to linear features. I used snow-tracking data collected from four wolf packs in the Central Rocky Mountains over 6 winters to test the hypotheses that wolves respond to linear features differentially, that linear features with relatively low levels of human activity influence wolf movement patterns by providing efficient travel routes, and that traffic volume affects the road crossing frequencies by wolves. I used 13 years of wolf mortality data to test the hypothesis that traffic volume affects level of automobile-caused wolf mortality. I also assessed the permeability of the Trans Canada Highway (TCH) and wildlife underpasses to wolf movements.

STUDY AREA

The study was conducted in portions of Banff National Park, Alberta, Kootenay and Yoho National Parks, British Columbia, Kananaskis Country Recreation Area, Alberta, and adjacent provincial land 1 January 1, 1987 and 30 April 2000 (Figure 4.1). Topographic and vegetative features are described in Chapter 2

Small towns, roads, developments, and timber harvest are scattered throughout the study area (Figure 4.1). Transportation routes in the study area consist of a major transcontinental highway and railway line, several secondary highways, and numerous access roads, rural, and forestry roads, which are described in Chapter 2. The TCH is four lanes wide and fenced for approximately 47.4 km of its length within the study area to deter wildlife from crossing the highway (Pacas 1996). Numerous wildlife underpasses and 2 wildlife overpasses exist along the fenced section to provide opportunities for wildlife to cross the TCH safely. Four additional secondary highways and numerous access roads and forestry roads exist within the study area and are one or two lanes without fencing or wildlife crossings.

Recreational trails and facilities are numerous in the study area. Banff National Park maintains approximately 145 km of cross-country ski trails, and contains an additional 150 km of ungroomed cross-country ski trails and 3 alpine ski areas. Kootenay National Park maintains approximately 42 km of cross-country ski trails and has 14 km of ungroomed trails; Yoho National Park has 42 km of groomed cross-country ski trails and 146 km of ungroomed ski trails, and Kananaskis Country maintains approximately 160 km of cross-country ski trails and 2 alpine ski areas. Numerous power lines also exist

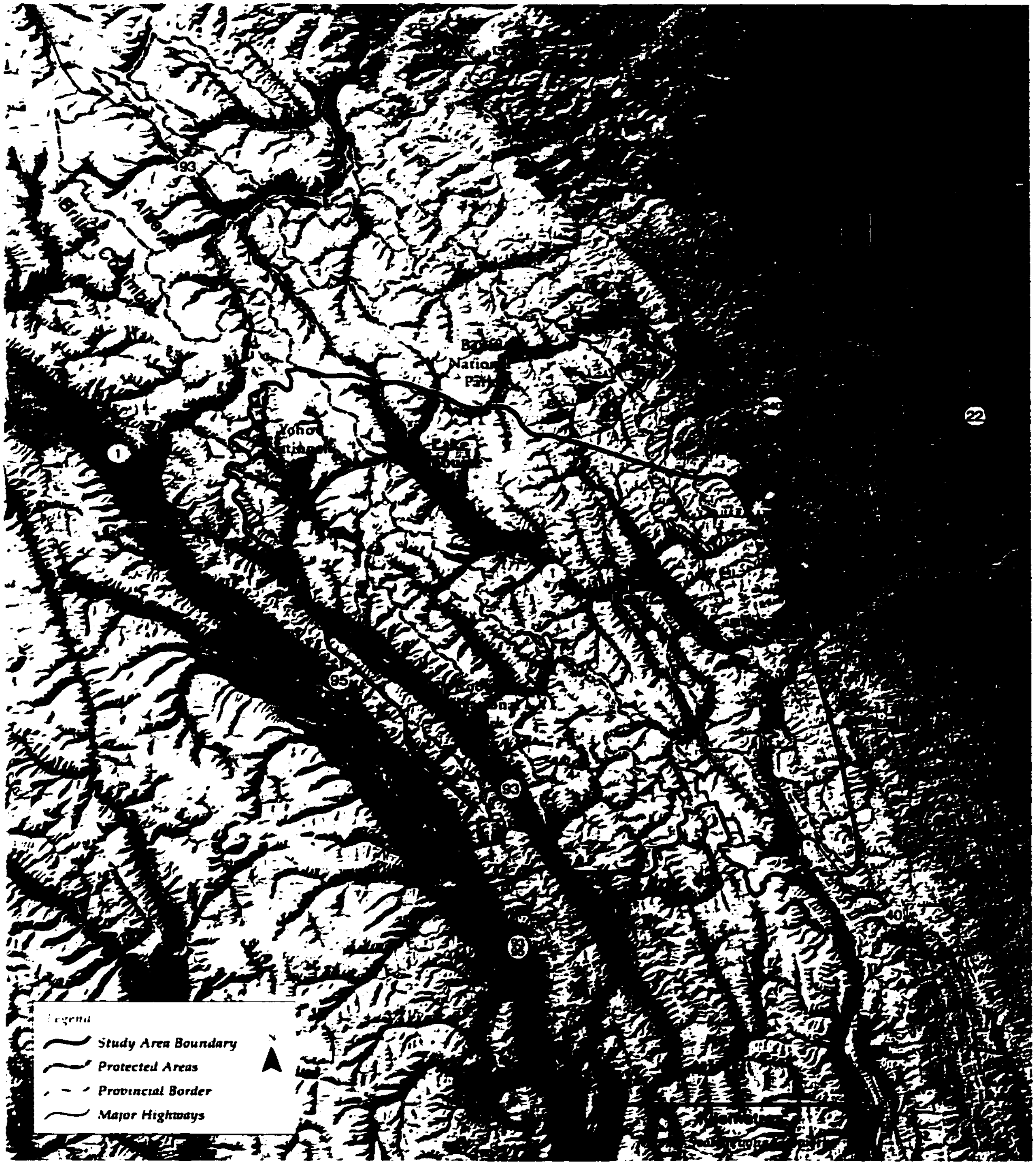

Figure 4.1. Study area in 10,000 km^2 of the Central Rocky Mountains, Canada.

within the study area. Powerline corridors are typically 30 m wide, and the areas underneath the lines are kept clear of brush and trees.

Six major rivers traverse the study area, including the Bow and Cascade Rivers in Banff National Park, the Vermilion and Kootenay Rivers in Kootenay National Park, the Kickinghorse River in Yoho National Park, and the Kananaskis River in Kananaskis Country.

METHODS

Data Collection

Fourteen wolves from 4 packs (Bow, Cascade, Kootenay, and Lougheed) were captured, radiocollared, and monitored (November 1 - April 30) between 1994 and 2000. Capture and immobilization methods are described in Chapter 2 and in Paquet (1993).

One to 3 wolves per pack were fitted with a radiocollar during all winters except for the Lougheed pack, which had no radiocollared members for 2 winters. Attempts were made to relocate collared animals every morning between November 1 and April 30 1994 to 2000, following the methods of Mech (1983). Once the radiocollared member(s) of a pack were relocated, transects were followed some distance from the radiotelemetry location (> 2 km) to intercept the tracks left by the pack. Observers travelled via snowshoes or skis. Once tracks were encountered, they were followed opposite to the direction of travel by the wolves (backtracked) to reduce disturbance by observers. If a pack had no radiocollared members during a winter, cross-valley transects were followed using skis or snowshoes until wolf tracks were detected.

Global Positioning System (GPS) units (Garmin International, Olathe KS) were used to collect waypoints as Universal Transverse Mercator (UTM) coordinates along tracks. The data were imported to a GIS (Idrisi, Clark University 1987) and entered into a database file. Tracking sessions were continued for consecutive days until snowfall, lack of snow, or avalanche hazard precluded further tracking. When wolf packs moved to more remote locations, collared wolves were relocated via aerial telemetry, and attempts were made to track wolves to the remote locations by following the tracks on skis.

When observers encountered wolf tracks that had approached and travelled on a linear feature, the following information about the event was collected: the type of linear feature (ploughed or unploughed road, compacted trail, or river), whether the individual(s) veered away from the feature without crossing, crossed directly, paralleled the feature prior to crossing, or travelled on the feature. If the tracks continued on the linear feature, observers recorded the compass bearing of the wolf tracks prior to approaching the feature, while travelling on the feature, and after exiting the feature. Observers also recorded the distance wolves travelled on the feature and, when possible, whether wolves used the feature at night or during the day. Observers were able to record night time use of linear features only if they confirmed no use at the end of one day and recorded activity on the feature early the following morning.

Digital road and trail data were obtained from Parks Canada and Alberta Environment (National Topographic Database Series, Ministry of Supply and Services Canada 1986). Road traffic data were obtained from Parks Canada (Table 4.1). Roads were classified into three types according to traffic volume (type I, average daily traffic volume (ADTV) > 6,000; type II ADTV >500 and <2,000; type III ADTV <500).

I used a GIS (Idrisi, Clark University 1987) to select random samples of 100 m tracking segments from snow tracking sequences for each pack and each year of data collection. The number of 100 m segments corresponded to the number of data points recorded for wolves approaching and travelling on linear features. I split each segment into 2-50 m sections and determined the angle of deflection between the 2 sections. These data were compared to the angle of deflection between the bearing that wolves travelled while approaching a linear feature and while travelling on the feature.

Data on automobile-caused wolf mortalities were collected opportunistically throughout the study area by visual sightings, mortality signals from radiocollared wolves, and through reports made by Parks Canada, Alberta Environment and British Columbia Ministry of Environment. Wolf mortality data were collected from 6 packs, including the Bow, Cascade, Kootenay, Lougheed, Yoho, and Saskatchewan Crossing packs.

Wildlife fencing and underpasses designed to move wildlife across the highway safely exist in a section of the TCH within the Cascade pack's territory. An ideal test of the effects of the TCH on wolf movement patterns is to determine the frequency that wolves cross the habitat that comprises the highway in the presence and absence of the highway. If the TCH was completely permeable to wolf movements, one could expect that wolves would cross the highway as frequently as if the highway were not present. Because such an experiment would require the removal of the highway, I chose an alternative methodology to test the permeability of the TCH to wolf movement. A line representing an 'invisible highway' was derived in a geographic information system (GIS, arcview) where wolf habitat use probability (Chapter 2) was not different on either side of the line and to habitat on either side of the TCH (Figure 4.2; t-test, equal variance not assumed, P=0.092). I assumed that the crossing frequency of the invisible highway should be equal to that of the TCH. To determine the permeability of the TCH, I compared the number of crossings of the invisible highway and the number of crossings of the TCH during the winters of 1995/96 and 1996/97. I also compared the use of wildlife underpasses between the Cascade pack and the Bow Valley pack over 2 winters.

To derive the invisible highway, an area adjacent to the TCH was defined, several polygons were drawn within the area, a random point was placed within each polygon, and the random points were connected using the animal movement module of Arcview. The invisible highway was 9.1 km long and approximately 0.13 – 0.88 km from the TCH in the Bow Valley of Banff National Park (Figure 4.2). I overlaid tracking sequences from 2 winters for the Cascade pack, whose territory incorporated the TCH and the derived line.

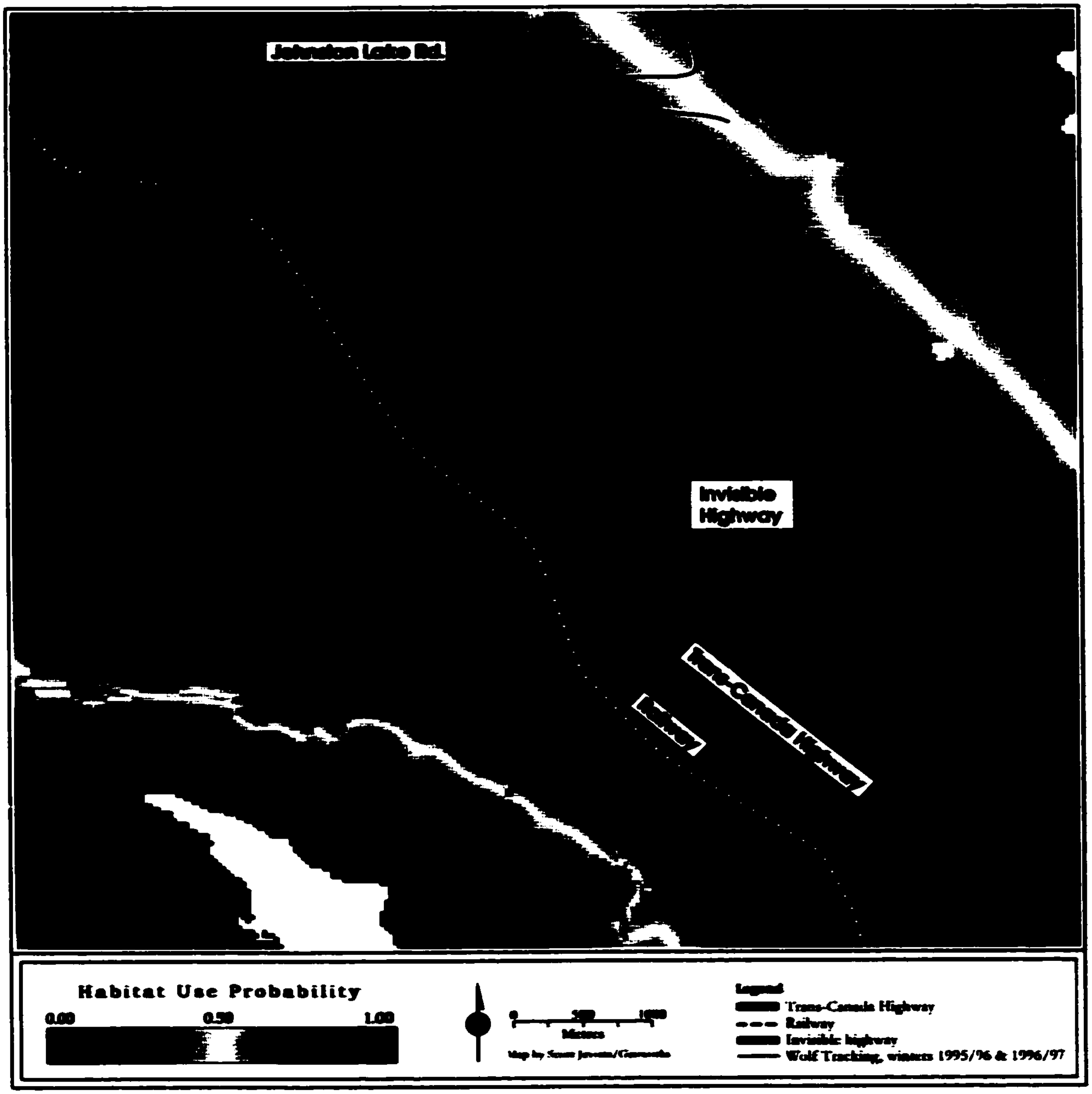

Figure 4.2. Location of invisible highway in relation to Trans-Canada Highway and movement patterns of the Cascade wolf pack, winter 1995/1996 - 1996/97.

Statistical Tests

To reduce the likelihood of inequality of error variances, I used an arcsine square root transformation of all proportional data (Zar 1996). All tests were computed using an alpha of 0.05. Statistical analyses were conduced in SPSS (Norusis 1990). Where *post hoc* tests were required, I used a Least Significant Difference (LSD) procedure to evaluate differences among specific means if the assumption of equal variance was met, or Tamahane's T2 procedure (Zar 1996) if the assumption was not met.

I used a General Linear Model (GLM, Ramsey and Schafer 1997) to compare the proportion of successful crossings (successful crossings/crossing attempts) among packs and type of linear feature (roads, compacted trails, and rivers). Because not all packs interacted with all linear features in every year, I used the mean proportions of successful crossings for each linear feature across years for each wolf pack (Table 4.2). I included pack and type of linear feature as fixed factors in the model. I used a GLM repeated measures design (Zar 1996) to test for a year effect for 1 pack that interacted with all linear features over the 6 years of the study.

To investigate whether wolves responded differentially to road type, I used similar methods in a GLM to compare the mean proportion of successful crossings among 3 road types for each wolf pack across years (Table 4.3). I included pack as a fixed factor in the model. Although no pack interacted with all road types for all years of the study, I used a GLM repeated measures design to test for a year effect for 2 packs that interacted with 2 road types each for 5 years of the study.

I used a GLM multivariate design to test whether linear features (roads, trails, and rivers) influenced the movement patterns of wolves. I compared the mean angle of deflection for each year between the bearing on the approach of a linear feature and the bearing while travelling on a linear feature, and the mean angle of deflection between pairs of adjacent segments from randomly selected tracking sequences (Table 4.4). I included pack and year as fixed factors.

I used a GLM to compare mean distance travelled on features for each year with pack and year as fixed factors as a test of whether the distance that wolves travel on linear features differs among type of linear feature (roads, rivers, and trails).

I used a GLM to compare number of wolf deaths per kilometre of road for each road type per year between 1987 and 2000 (Table 4.5) with year as a fixed factor.

I tested for differences between the crossings of the invisible highway derived in GIS to the crossings of the TCH using the G-test (Sokal and Rolf 1995). I used the Williams' correction to reduce type I error (Sokal and Rolf 1995).

RESULTS

Average traffic volume on roads in the study area varied between 147 and 7,052 automobiles per day (Table 4.1). Traffic volume data were not collected for the rural and forestry roads in the study area, although traffic volume on these roads was likely much lower than on the highways (S. Donelon, AB Department of Community Development, pers. comm., B. Forbes, B.C. Ministry of Environment, pers. comm.).

Table 4.1. Average daily traffic volume on highways in the Central Rocky Mountains between 1994 and 2000 (Parks Canada unpublished data; Alberta Ministry of Transportation unpublished data).

Road	Average Daily Traffic Volume (+/- SD)	Road Type
TCH*	7,052 (678)	I
Hwy 40+	1,901 (283)	II
Hwy 93S++	1,764 (467)	II
Hwy 93N	1,565 (329)	II
Minnewanka Loop	463 (495)	III
Hwy 1A+++	243 (254)	III
Smith Dorien Hwy	147 (91)	III

*Castle Junction Counter; + Barrier Lake Counter;
++ Settler's Road Counter; +++ BVP east monitor

The proportion of successful crossings did not differ among type of linear feature (Table 4.2; GLM, $F_2 = 0.30$, $P = 0.75$). No pack effect was detected (GLM, $F_3=0.61$, $P=0.63$). A difference among years was detected for the Lougheed pack (GLM repeated measures, $F_4 = 946.20$, $P = 0.02$).

The proportion of successful crossings varied by road type (Table 4.3; GLM, $F_2 = 5.31$, $P=0.04$) but there was no effect of pack (GLM, $F_3 = 0.01$, $P=0.10$). Differences were significant in mean proportion of successful crossing between road type 1 and 3 (LSD $P=0.01$). No difference among years was detected for the Bow pack (GLM repeated measures, $F_4 = 7.95$, $P=0.81$) or the Lougheed pack (GLM repeated measures, $F_4 = 0.10$, $P=0.81$).

Angles of deflection differed for wolves travelling onto linear features and those derived from random segments of tracking sequences (Table 4.4; GLM, $F_2=84.72$, $P<0.001$). There was no effect of linear feature type (GLM, $F_2=0.771$, $P=0.55$) or pack effect (GLM, $F_3=0.76$, $P=0.61$). There was a year effect, however (GLM, $F_4 = 5.50$, $P=0.001$). A significant difference in mean angle of deflection occurred between year 2 and 5 (LSD $P=0.01$) and year 3 and 5 (LSD $P=0.001$). Of 127 events recorded from wolves travelling on linear features when the time of travel was known, 87% (110) occurred at night.

Distance travelled on linear features did not differ among type of linear feature (GLM, $F_4=2.17$, $P=0.09$). No pack effect was detected (GLM, $F_3=1.89$, $P=0.13$), but a year effect was detected (GLM, $F_4=3.67$, $P=0.01$).

Table 4.2. Mean proportion of successful crossing of linear features by wolves in the Central Rocky Mountains between 1994 and 2000.

	Road		River		Compacted Trail	
Pack	*n*	crossing	*n*	crossing	*n*	crossing
Bow	307	0.87	48	0.93	22	0.75
Cascade	88	0.80	17	0.90	21	0.92
Kootenay	44	0.85	14	0.85	4	0.75
Lougheed	91	0.79	16	0.75	34	0.88

Table 4.3. Mean proportion of successful crossing of roads by wolves in four packs in the Central Rocky Mountains during winter between 1994 and 2000.

	Road Type I*		Road Type II*		Road Type III*	
Pack	*n*	crossing	*n*	crossing	*n*	crossing
Bow	46	0.82	7	0.75	254	0.87
Cascade	7	0.55	-	-	82	0.97
Kootenay	-	-	26	0.79	18	0.87
Lougheed	5	0.60	25	0.90	61	0.87

* Road Type I traffic volume > 6,000 automobiles per day, Road Type II > 500 and < 2,000 automobiles per day, Road Type III < 500 automobiles per day.

Table 4.4. Mean angle of deflection for wolves approaching versus travelling on linear features, compared to mean angle of deflection for pairs of adjacent segments from randomly selected wolf tracking sequences for four wolf packs in the Central Rockies during winter 1994 – 1999.

Feature	Year	Pack	Mean Angle Deflection (SD)	Mean Random Deflection (SD)	*n*
Road	1995/96	Bow	36.2 (26.9)	9.6 (12.4)	13
Road	1996/97	Bow	57.2 (38.3)	13.4 (13.6)	5
Road	1995/96	Cascade	53.3 (29.3)	15.2 (20.3)	13
Road	1996/97	Cascade	79.5 (40.1)	1.7 (2.8)	11
Road	1996/97	Kootenay	66.3 (28.6)	7.6 (15.1)	11
Road	1998/99	Kootenay	44.3 (34.1)	1.2 (2.5)	9
Road	1996/97	Lougheed	58.4 (42.8)	13.4 (13.5)	10
Road	1998/99	Lougheed	38.8 (33.0)	8.0 (12.3)	4
River	1995/96	Bow	36.7 (15.3)	3.3 (2.1)	3
River	1995/96	Cascade	37.5 (13.7)	5.0 (5.6)	6
River	1995/96	Lougheed	81.7 (32.5)	19.7 (25.4)	3
River	1996/97	Lougheed	47.5 (46.0)	19.5 (27.6)	2
River	1998/99	Lougheed	22.0 (13.4)	0.0 (0.0)	2
Trail	1995/96	Bow	48.8 (38.6)	10.1 (12.9)	12
Trail	1996/97	Bow	57.5 (31.8)	2.5 (3.5)	2
Trail	1995/96	Cascade	53.1 (36.1)	13.6 (23.8)	31

Trail	1996/97	Cascade	51.2 (36.4)	8.2 (14.3)	5
Trail	1996/97	Kootenay	55.0 (46.6)	6.9 (12.1)	18
Trail	1998/99	Kootenay	13.5 (2.1)	0.0 (0.0)	2
Trail	1995/96	Lougheed	63.6 (40.9)	21.0 (21.1)	10
Trail	1996/97	Lougheed	64.6 (55.5)	11.0 (2.0)	15
Trail	1998/99	Lougheed	38.8 (36.9)	6.1 (2.7)	12

Automobiles caused the death of 53 wolves between 1987 and 2000. Of these, 15 were pups, 3 were yearlings, and 35 were adults. Most of the pups (60%) and adults (56%) died in the summer and fall.

Wolf deaths per km over 14 years differed among road types (Table 4.5; GLM, F_2=9.37, P<0.001), especially between road type 1 and 2 (T2, P=0.023) and road type 1 and 3 (T2, P=0.001). No year effect was detected (GLM, F13=1.53, P=0.13). Differences were detected in wolf deaths per km between specific roads.

The Cascade wolf pack crossed the 'invisible highway' derived using GIS on 26 occasions during the winter of 1995/96 (Figure 4.2). In comparison, members of the Cascade pack made 1 successful crossing and 3 failed attempts to cross the TCH during the winter of 1995/96 after crawling through a hole in the wildlife fencing. During the winter of 1995/96, the Cascade pack also made 3 failed attempts to use wildlife underpasses to cross the TCH, whereby wolves traveled to the entrance of an underpass but veered away. The Cascade pack crossed the invisible highway on 17 occasions during the winter of 1996/97 (Figure 4.2). In comparison, members of the Cascade pack made 1 successful crossing and 2 failed attempts to cross the TCH during the winter of 1996/97 after crawling through a hole in the wildlife fencing. One of the failed attempts resulted in the death of a wolf due to a collision with an automobile. The wolves also made 2 successful crossings and three failed attempts to

Table 4.5. Wolf deaths per km of road in the Central Rocky Mountains. Wolf mortality data collected between 1987 and 2000.

Road	Road Type*	Deaths	Kilometres	Deaths/km/14 years
TCH	I	25	139	0.0128
93S	II	17	96	0.0126
93N	III	5	76	0.0047
1A	III	2	58	0.0025
40	II	1	107	0.0007
Logging	III	2	493	0.0003

*Refers to traffic volume: I > 6,000, 500<II<2,000, III<500 cross the TCH using wildlife underpasses during the winter of 1996/97. A significant difference between observed and expected crossings of the TCH was detected (G test X^2=3.841, p<0.001). The mean permeability of the TCH was 10.7% for the Cascade wolf pack over the 2 winters.

The response of wolves to underpasses appeared to vary among wolf packs. During the 2 winters of 1995/96 and 1996/97, members of the Cascade wolf pack attempted to use underpasses on 8 occasions, resulting in 2 (25%) successful crossings. In contrast, the Bow Valley pack made 27 attempts to use underpasses during the same period, resulting in 24 (89%) successful crossings.

DISCUSSION

The behavioural response of wolves to linear features they encounter in the winter landscape may be described as a complex array of repulsion-attraction, influenced by the magnitude and timing of human activity on the linear features. Linear features may at times be physical or psychological impediments to wolf movement and, at other times, be used by wolves for efficient travel through a snowy environment.

A repeated measures design would have been the ideal approach to testing the response of wolf packs to linear features because crossing events within a pack are not likely to be independent. One event may lead to greater sensitivity in the pack's response to linear features. For example, the Spray pack's use of underpasses decreased dramatically for several months following the death of the pack's alpha female on the TCH in 1990 (P.

Paquet unpublished data). Alternatively, packs may become less sensitive to linear features over time. Because some packs did not interact with all types of linear features in all years, the data were too limited to use the repeated measures design. Where I could use a repeated measures GLM to test for differences among years, I found an effect of years within one pack in crossing success of all linear feature types. One case, however, does not allow for easy generalization of a year effect. The source of variation from year to year may be related to variable snow conditions. Two winters of the 6 studied were high snow years with colder than average temperatures, and 2 winters had low snow accumulation and milder than average temperatures (Environment Canada unpublished data). I did not find a year effect in crossing success among road types for the two packs I was able to use a repeated measures design. In future studies, data should be collected from more packs to address the question of independence among crossing events.

My data indicate that the crossing success rate was similar for roads, rivers, and trails, and the behaviour of wolves to linear features was consistent among the four wolf packs. Although one might expect that a river would be successfully crossed during each attempt, changing ice conditions and water flow likely reduce the permeability of rivers to wolf travel. When the river was not frozen, wolves often paralleled the shoreline to a convenient point of crossing (e.g., ice bridge or short distance between shores). On occasion wolves crossed the river by swimming.

Road crossing success was related to traffic volume. The success rate of wolves attempting to cross roads with traffic volume > 6,000 automobiles per day was significantly lower than that of wolves attempting to cross roads with a low average daily traffic volume (<500 automobiles per day). The frequency of traffic affected road-crossing success because animals need sufficient time between successive automobiles to cross the road successfully.

Wolves tended to change their direction of travel to use compacted roads and trails and this pattern of direction shift was not detected from random tracking sequences. This suggests that wolves were attracted to linear features in the winter. These features influenced movement patterns, and wolves responded similarly to roads, rivers, and trails. Human activities that modify snow compaction, including cross-country skiing, snowmobiling, and ploughing roads, evidently influence winter movements of wolves by providing travel routes that are energetically less demanding than unmodified routes. Paquet et al. (in review) also determined that wolves in the Central Rockies selected human modified trails over unmodified wildlife trails, and that these modified trails often traversed areas where snow conditions would otherwise have restricted or precluded wolf movements. Other studies have shown similar attractions of wolves to compacted roads and trails during winter (Formozov 1946; Green 1951; Mech 1970; Zalozny 1980; Bjarvell and Isakson 1982; Paquet 1993). The influence of human activity on winter wolf movements may alter wolf-prey relations by facilitating movements between patches of prey (James and Stuart Smith 2000;Paquet et al. in review). On several occasions, for example, the Cascade wolf pack killed moose (*Alces alces*) or elk (*Cervus elaphus*) in areas with deep snow conditions after travelling on a compacted ski trail for several kilometres.

A year effect was detected in the mean deflection onto linear features. A *post hoc* investigation of snow accumulation data revealed that differences occurred between high and low snow years. Snow accumulation was high during the second and third winters of the study, and mean deflection onto trails was also higher (51.4 deg. and 59.7 deg.) than during the fifth winter of the study (31.5 deg.), which had low snow accumulation. Linear features that wolves can use to their advantage for travel thus appear to have a greater influence on wolf movements during high snow pack conditions.

Although wolves in the Central Rockies tend to be diurnal in their winter activities (M. Percy unpublished data), most of the use of linear features by wolves was made at night. On numerous occasions, for example, the Cascade wolf pack bedded near a popular ski trail in the Bow Valley during the day, where they were out of view of skiers, and travelled on the trail at dusk or during the night to access the Cascade Valley. The Lougheed pack similarly timed their regular returns to the Kananaskis Valley such that they travelled on cross-country ski trails at night. My results suggest that wolves may alter their patterns of activity to allow use of compacted trails and ploughed roads when the risk of human disturbance is low.

High traffic volume roads increased the risk of mortality to wolves. Automobiles on road type I (TCH) caused significantly more wolf deaths per km than the other road types. During summer 2000, traffic volumes on the TCH in Banff National Park were as high as 15,800 automobiles per day in the unfenced section of the highway and 29,000 automobiles per day in the fenced section (Parks Canada unpublished data). Hourly traffic volumes in the unfenced section during mid-day in July 2000 were as high as

2,533 automobiles, which translates to 21 automobiles per minute or approximately 1 automobile per 3 seconds on each side of the highway. These traffic volumes represented the extreme conditions during 2000 and are obviously too high to allow wolves to cross. Traffic volume on the TCH has increased 3.7% per year from 1982-1994, and is projected to increase to an average annual daily traffic volume of 25,262 by 2010 (Pacas 1996). Traffic volume on all major access routes to Banff National Park, including Highway 93S, is also increasing. This suggests that the proportion of successful road crossings will decline and the risk of wolf mortality will increase.

Although one study documented that black bears (*Ursus americanus*) in non-mountainous systems select home ranges that do not include roads of high traffic volume (Brody and Pelton 1989), the limitations imposed on habitat availability by mountainous terrain may preclude this option for large mammals. Topographical complexity in mountainous areas influences the spatial distribution of animals by concentrating the activities of wolves and their prey to lower elevations, which coincides with road placement (Chapter 2). Scale is also an important consideration in assessing effects of roads. Species that have large home ranges or long distance dispersal requirements, such as wolves, are more sensitive to linear development effects than are species with smaller area requirements because the probability of encountering a road is much greater for species that range over a broad area (Jalkotzy et al. 1997).

Traffic speed may also increase risk of mortality to wolves. Traffic speeds on the TCH and on Highway 93S, are the highest in the study area. During the year 2000, 85% of traffic on the TCH and 88% of traffic on Highway 93S exceeded the speed limit of 90 km/hr, and 19% of traffic on the TCH and 16% of traffic on Highway 93S exceeded 110 km/hr (Parks Canada unpublished data). Coincidentally, wolf deaths per km of road on Highway 93S (0.126) and on the TCH (0.128) were the highest in my study area and did not differ significantly (P= 0.875). Because Public Works Canada and the Alberta Ministry of Transportation did not record traffic speed on most of the highways in the study area, data are inadequate to conduct a full analysis of the relationship between traffic speed and risk of mortality to wolves. Future research should address this deficiency.

More wolves were killed by automobiles during summer and fall, which coincides with the denning season and early forays with the pups from the den, as well as with the highest traffic volumes of the year (Parks Canada unpublished data). Of the 16 den sites used by the 5 packs from which mortality data was collected, 12 (75%) were within 1 km of a road. Adults travelling to and from a den that was close to a road were more exposed to the risk of road mortality than adults occupying den sites in remote locations. Pups making hunting forays with adults were also exposed to the risk of mortality, but without the ability to move as quickly as adults or the life experience to avoid hazards. During an excursion that the Bow Valley pack took from their den in the Spray Valley south of Banff town site to Kootenay National Park in August 1996, the pack crossed the TCH on four occasions and crossed Highway 93S twice. Three of the four pups in the litter were killed by automobiles during these road crossings.

The TCH impeded movements of the Cascade wolf pack, and wildlife underpasses were not successful in encouraging the pack to cross the highway safely. The response to underpasses appears to vary with pack, and the Cascade pack had a greater negative response to underpasses than the Bow Valley pack. On two occasions, the Cascade wolf pack chased an elk along the TCH fence and the elk escaped through an underpass. The pack did not enter the underpass on either occasion. The sensitivity of the Cascade pack to the TCH may have decreased with time, but the pack shifted its home range away from the TCH in late winter 1996/97. Although the shift in home range may have been a response to decreased prey density, a high concentration of elk on the south side of the TCH remained available but unexploited by the pack. Clevenger and Waltho (2000) determined that wildlife underpasses in the Banff Bow Valley function less effectively for carnivores such as wolves than for ungulates.

Anthropogenic alterations of habitat have significant influences on winter wolf movements and on wolf survival. My data showed that, although wolves can use roads as travel corridors, crossing success and survival decrease as traffic volume increases. Although my study did not address the ecological significance of altering wolf movement patterns, its observations suggest the potential for cascading effects. The relationship between habitat use, prey distribution, and topography could be perturbed, dispersal patterns and use of movement corridors altered, access to winter ungulate ranges facilitated or impeded, and movements of wolves outside protected areas encouraged. Wildlife managers should incorporate the potential effects of linear features on wolf survival, movements, and wolf-prey relations in the planning process. Future studies of wolf-prey interactions should account for the potential confounding influence of human-modified snowy landscapes, whereby the killing rate of wolves may be higher due to increased access to prey provided by roads.

A contemporary challenge facing conservation biologists is to understand the response of wildlife to anthropogenic change (Pettifor et al. 2000). Ims (1995) suggested that neither theory nor empirical knowledge of animal movement patterns is sufficiently developed for testing questions about the relationship between spatial structure and movement patterns. Snow tracking may provide a useful tool, and likely exceeds the utility of conventional radio collars, to assist in the development of biologically realistic models that accurately predict animal movement patterns in response to spatial structure and human disturbance.

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CHAPTER 5

LINKING SOCIAL BEHAVIOUR TO A POPULATION VIABILITY ANALYSIS FOR A GRAY WOLF POPULATION IN THE CENTRAL ROCKY MOUNTAINS

INTRODUCTION

Small populations are vulnerable to decline due to stochastic processes (Shaffer 1981; Gilpin and Soulé 1986). Deterministic effects of human-caused mortality may also be important for populations of some species (Caughley 1994; Groombridge 1992), especially large carnivores, because of their low densities and wide-ranging movements (Woodroffe and Ginsberg 1998). The ranging behaviour of large carnivores exposes them to risks of mortality along the borders of protected reserves, such that even populations that are protected, in principle, by reserves experience human-caused mortality in areas adjacent to reserves. A reduced population size, causing lower resiliency to stochastic processes and extinction, may be the result of these edge effects (Woodroffe and Ginsberg 2000).

Carnivores that live in social groups may be more liable to suffer edge effects than solitary carnivores because of reproductive suppression, where the number of breeding units in a population is typically restricted to the number of social units (Caro and Durant 1995). The effects of demographic stochasticity may be greater for socially breeding species with a small number of breeding groups (Vucetich et al. 1997). Although the social behaviour of species and their response to human activities can have important implications for population viability (Tuyttens and MacDonald 2000), few attempts have been made to understand the relationship between behaviour and persistence (Durant 2000). To do so requires a model that incorporates the behavioural life history complexities of the species of interest.

Dispersal behaviour and social organization are illustrations of life history complexities that likely have important consequences for population persistence of social carnivores. Wolves, for example, live in extended family social groups (packs) that occupy territories and are characterized by reproductive suppression and complex dispersal patterns (Mech 1970; Zimen 1976; Packard et al. 1983; Boyd and Pletscher 1999). The structure of wolf populations may be described as fitting the metapopulation paradigm (Levins 1970; Hanski 1991) because packs function as subpopulations within a larger population, and may go extinct over time (Mladenoff 1995). Furthermore, movement of individuals among packs is likely an important factor in population persistence (Haight et al. 1998).

Most of the earlier attempts at modeling wolf population dynamics used models that did not adequately incorporate the social breeding or dispersal aspects of wolf biology (Keith 1983; Fuller 1989; Kelly et al. 1999; Ewins et al. 2000). Those that incorporated some detailed aspects of these behaviours found an effect on persistence (Boyce 1993a; Haight et al. 1998; Vucetich et al. 1997). No model has been developed, however, that allows the behaviour of individuals to respond to social conditions of the pack. Because these aspects of wolf biology are believed to have important implications for persistence

(Vucetich et al. 1997), incorporating them into simulation models for wolf populations will allow for testing whether they actually do govern population dynamics.

A population viability workshop, held in June 2000, focused on the challenge of modeling the persistence of a low-density population of wolves that is exposed to human-caused mortality and occupies protected and non-protected habitat in the naturally fragmented topography of the Central Rocky Mountains. The challenge was approached by building an individual-based model (DeAngelis and Gross 1992), MORTA (Vucetich et al. 2002), with detailed social and dispersal components that integrated population parameters and demographic and environmental stochasticity.

Knowledge of the relationship between edge effects and persistence of carnivore populations may have implications for protected reserve design and management. Edge effects may be greater in populations of social carnivores where a high proportion of social units are distributed along the protected reserve borders. This study investigated the interaction of wolf social dynamics and population parameters, evaluated whether the observed patterns of mortality within and adjacent to protected reserves is sufficient to drive the local population to extinction, and explored which demographic parameters may be the most sensitive to population persistence. The inferences drawn from the analyses may also yield insights into the interactions between behaviour and population persistence among other social carnivores.

STUDY AREA AND POPULATION

This study was conducted in portions of Banff National Park, Alberta, Kootenay and Yoho National Parks, British Columbia, Peter Lougheed Provincial Park, Alberta, and portions of British Columbia and Alberta adjacent to these protected areas between 30 April 1987 and 31 December 2000 (Figure 5.1). The study was initiated in the Bow River Valley following the natural recolonization of the valley by two wolf packs. As the population increased, the study area was expanded to eventually cover 18,670 km^2 of the Central Rocky Mountains.

Topographical and vegetative features, and prey species are described in Chapter 2. Small towns, developments, and timber harvest are scattered throughout the study area (Figure 5.1). A railway line, a primary highway and numerous secondary highways, tourist access roads, rural, and forestry roads exist within the study area and are described in Chapter 2.

Seven protected areas totalling 10,159 km^2 occur within the study area, including Banff, Kootenay, and Yoho National Parks, and Peter Lougheed, Bow Valley, Spray Lakes, and Canmore Nordic Centre Provincial Parks. Hunting or trapping wolves is not permitted within these protected areas. The Provinces of Alberta and British Columbia regulate wolf hunting and trapping elsewhere in the study area and regulations are described in Chapter 3.

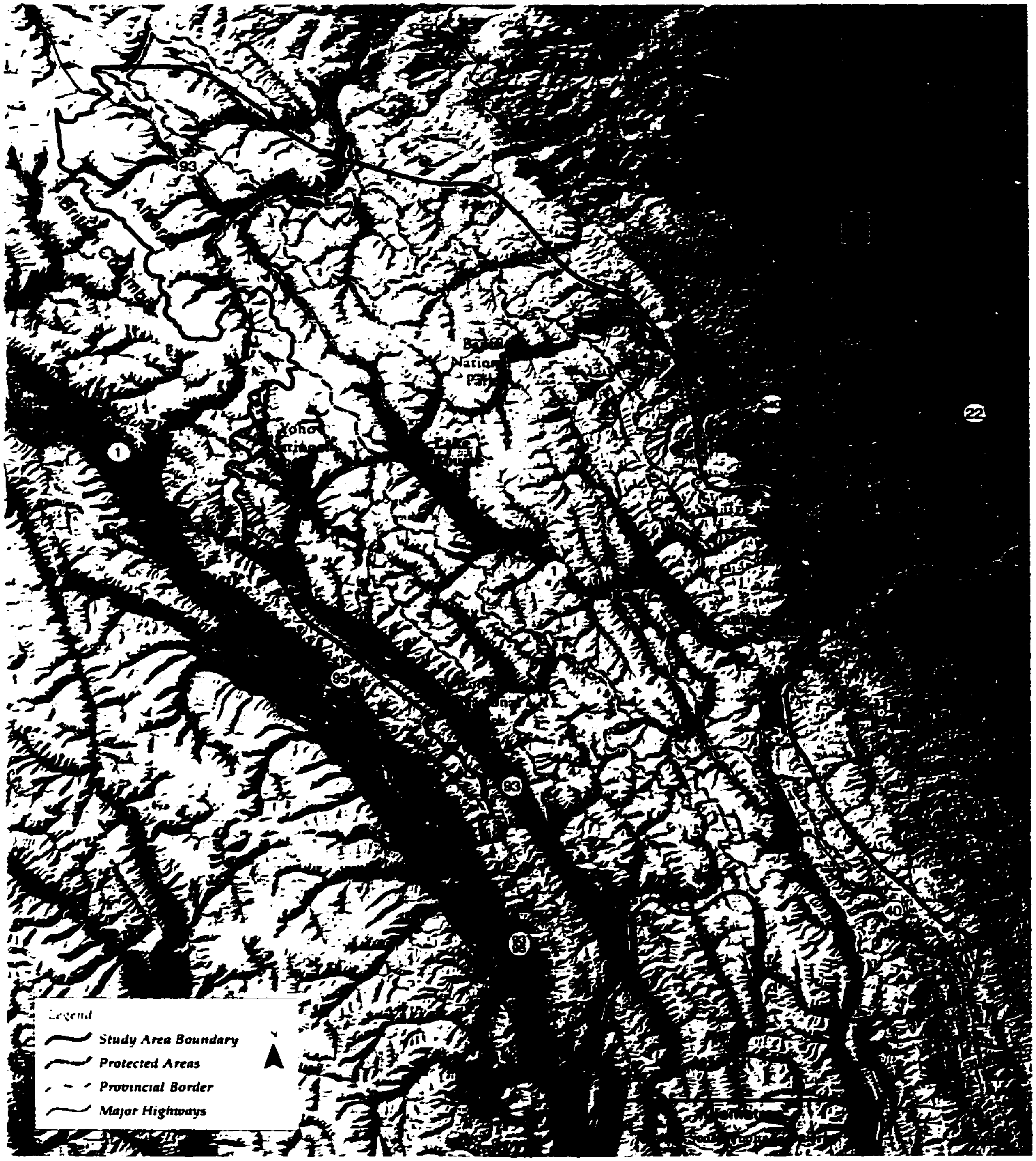

Figure 5.1. Study area in 18,700 km^2 of the Central Rocky Mountains, Canada.

Wolves were extirpated or severely depleted twice during the 20th century in the Central Rockies (Paquet 1993). Wolves were very scarce by the early 1900s, and most were eliminated by 1914 (Cowan 1947). Natural recolonization occurred during the 1930s (Cowan 1947), and by the 1940s full reestablishment of the population was believed to have occurred (Green 1951). An extensive predator control program in Alberta, British Columbia and the four mountain national parks between 1952 and 1956 eliminated wolves from most of the Central Rockies (Ballantyne 1956; Gunson 1992; Mickle et al. 1986). Recolonization occurred between the mid-1970s and the early 1990s (Holroyd and Van Tighem 1983; Poll et al. 1984; Paquet 1993; Parks Canada unpublished data). By the mid 1990s, twelve packs had established in the study area (Paquet and Callaghan unpublished data).

METHODS

Field Studies

Forty-two wolves from 12 packs were captured, radiocollared, and monitored between 1987 and 2000. Capture, immobilization, and monitoring methods are described in Chapter 2 and 3.

Annual wolf survival was estimated using the radiocollared sample and the nonparametric Kaplan-Meier method (Kaplan and Meier 1958), staggered entry design (Pollock et al. 1989; Chapter 3). Reproduction was estimated via den site observations conducted each year between 1990 and 2000. Information on dispersal and ascension of dominance within packs was gathered using information from the present study (which included 15 radiocollared dispersing wolves) and obtained from studies conducted in Yellowstone National Park (D. Smith National Parks Service pers. comm.) and the northern Rockies (Pletscher et al. 1997; Boyd and Pletscher 1999). Mid-winter population censuses were conducted on most of the population each year via aerial and ground tracking techniques and in cooperation with the Banff National Park Warden Service annual sensitive species survey.

Radiotelemetry data from 8 wolf packs and the adaptive kernel method (Worton 1989) (95% isopleth) were used to derive home range polygons in the program Calhome (Kie et al. 1994). These results were used to estimate the average home range size of wolf packs in the Central Rockies.

Description of MORTA

MORTA (Vucetich et al. 2002) is an individual-based, age-structured, spatially implicit stochastic simulation program of the population dynamics of wolves or other social carnivore species. In the simulation, each individual belongs to either a pack (capable of reproduction) or a collection of dispersers (not capable of reproduction). A population consists of one or more packs and one group of dispersers. Individuals within each group are characterized by the same set of vital rates, but annual survival and dispersal rates may be age- or sex- specific.

The model includes demographic and environmental stochasticity (including catastrophes), population and pack-level density dependence, and temporal variations in environmental carrying capacity (K) at the pack and population level. The process of demographic stochasticity is simulated via a random number generator to determine the occurrence of probabilistic events such as reproduction, litter size, sex determination, and mortality. Simulations occur in discrete time steps of one year. The model steps through a sequence of events that describe the typical life cycle of social carnivores such as wolves.

Model Structure and Parameters

The model was designed to simulate a wolf population occupying protected reserves (i.e. national and provincial parks) and non-protected lands in the Central Rocky Mountains. Demographic parameters were estimated from data collected over 13 years from a wolf population occupying the Central Rocky Mountains (Table 5.1). Habitat that is suitable for wolves is limited in the Central Rockies (Chapter 2), and consequently wolves occupy large home ranges, averaging 1,709 km^2 (Table 5.2). The model focused on an area of the Central Rockies consisting of 18,670 km^2, where 12 pack territories exist (Figure 5.1). The model was thus bounded by the assumption that the population could support a maximum of 12 pack territories. I modeled quasi extinction by setting the minimum number of packs to two, assumed to be the lowest acceptable population size in the context of managing protected areas. Extinction risk was defined as the median proportion of extinctions out of 1,000 simulations.

Table 5.1. Model parameter estimates, used for baseline model.

Parameter	Estimate	sd
Juvenile Survival Rate[1]	0.52	0.36
Juvenile Disperser Survival Rate[2]	0.30	0.10
Adult Survival Rate Protected Packs[1]	0.89	0.19
Adult Survival Rate Border Packs[1]	0.72	0.16
Adult Disperser Survival Rate[3]	0.66	0.10
Mean Litter Size[1]	4	2.09
Range Litter Size[1]	0 – 8	___
Litter Sex Ratio (M:F)[1]	0.45:0.55	___
Minimum Breeding Age[2]	2	___

1 based on empirical data from the present study
2 based on little empirical data from the present study
3 estimate taken from Pletscher et al. (1997)

Table 5.2. Home range size of eight wolf packs occupying the Central Rocky Mountains, determined through adaptive kernel 95% isopleth method.

Pack	Home Range Size (km^2)
Bow	2581
Cascade	1098
Clearwater	801
Highwood	1172
Kootenay	2521
Lougheed	2852
Panther	1459
Yoho	1185

The protected reserves in the Central Rockies are comprised of terrain that is more rugged than provincial land adjacent to the reserves (Carroll et al. 2000). As a consequence, the territories of most wolf packs straddle protected reserves and adjacent provincial land that is less rugged, but where wolves are not protected from hunting or trapping by humans. The territories were identified in the model as being one of two pack types: protected or border packs, whereby the extent of the range of movements of protected pack members occurred within protected areas and movements of border pack members spanned protected and non-protected areas. Mortality data collected over 13 years from wolves in the Central Rockies indicates that survival is lower for wolves occupying border territories than those occupying protected territories (Table 5.1; Chapter 3). Currently, 2 wolf packs fully occupy protected areas and 10 packs occupy areas that border protected and non-protected areas. Because 1 of the 10 border packs occupies an area where only bow hunting is permitted, which rarely constitutes a risk of mortality to wolves, I considered this pack to be protected.

I estimated the distribution of litter sizes based on 63 litters from 11 packs observed in June 1989 - 2001 (Table 5.3). Because litter size did not differ significantly between pack types (Wilcoxon signed ranks test, P=0.126), I pooled the data for both pack types. I assumed that wolves occupying territories that were fully protected experienced lower human-caused mortality but that other vital rates were the same among pack type.

Table 5.3. Litter size distribution for the Central Rockies wolf population, 1989 - 2001.

Litter Size	Probability for First Litter*	Probability for Second Litter*
0	0.095	0.85
1	0.032	0.05
2	0.143	0.05
3	0.079	0.05
4	0.175	0.00
5	0.206	0.00
6	0.206	0.00
7	0.032	0.00
8	0.032	0.00

* Based on den site observations of 63 litters.

The baseline model, which represented parameter estimates and a model configuration that most closely approximates current conditions, incorporates 9 border packs and 3 protected packs. By varying the number of protected versus border packs, however, I estimated the number of protected packs required to maintain a population with less than 10% chance of extinction over 100 years in the absence of immigration. From this estimate, I calculated the areal expanse of pack territories to determine the size of reserve required to maintain the optimal number of packs without the influence of human-induced mortality in areas that border protected areas currently.

Model Sequence of Events

The following sequence of events was applied within each simulated year: Reproduction, Survival, Aging, Dispersal, Challenges to Dominance, and Ascension to Dominance. The distribution of wolves in the population was updated each year by moving the surviving wolves of each age class to the next class.

Reproduction

A litter of pups was produced each year if a breeding pair was present in the pack. Minimum breeding age was assumed to be 2 years of age. Litter size followed a discrete probability distribution (Table 5.3) with a mean of 4.0 pups and a range of 0 - 8 pups (Table 5.1). If a pack produced one litter of pups, then a second litter was produced, provided the pack had an additional pair of wolves. The maximum number of pups produced in a second litter was set to three, the range was 0 – 3, and the probability of the size of the second litter followed a discrete probability distribution from my observations

(Table 5.3). The probability that each pup was a male was assumed to be 0.55 based on the observations of 63 litters in the present study (Table 5.1).

The first litter of each pack was produced by the primary reproductive pair (one male and one female). The identity of the primary reproductive pair remained the same from year to year within each pack unless either one of the pair died or his/her breeding position was taken over by another individual within the pack. The second litter was produced by a randomly selected pair of wolves. The individuals that comprised the second reproductive pair varied independently each time a second litter was produced.

Immigration and Emigration

The disperser pool was comprised of a collection of non-breeding individuals that entered the pool as dispersers from a pack within the population or as immigrants from outside of the population. The rate of wolf dispersal may be independent of population density but related to mean pack size (Hayes and Harestad 2000). This aspect of wolf biology was modeled in MORTA by allowing each non-reproductive wolf belonging to a pack to disperse from its pack during each year of the simulation with an age and pack size - dependent probability (Table 5.4; Table 5.5). A probability distribution controlled whether each dispersing wolf was removed from the population, and this removal represented either long-range dispersal out of the population or mortality associated with dispersal. Most (71%) of the radiocollared dispersers in the Central Rockies permanently left the protected area that their natal pack occupied (Table 5.6). Consequently, simulations were structured to obtain a high probability for either long-range dispersal out of the population or mortality associated with dispersal. Each disperser was assigned a probability of 0.10 to leave the population immediately following dispersal and allowed 5 attempts per year to leave the disperser pool with 0.05 probability of dispersing beyond a protected area or dying during each attempt. Reproductive wolves (i.e., the primary reproductive pair and the parents of a second litter if one exists) were not permitted to disperse.

For the baseline simulation, 2 immigrants from outside the population entered the group of dispersers annually (Table 5.7). By varying the maximum number of immigrants, I investigated the role of immigration in population persistence. I assumed the probability of each new immigrant being a male was 0.50, and the age of each immigrant was determined randomly from a distribution of ages.

The maximum size of the disperser group was modeled as a reduction in survival as the group approached the maximum size. Individuals that were removed from the population in this manner were assumed to have either died or dispersed from the population (i.e., long-range dispersal). The proportion of dispersing wolves in a population reported in the literature varies from 2 – 28% (Fuller 1989). I assumed the K for the disperser pool was 15% of the population for baseline simulations (Table 5.7).

During each year of the simulation, each wolf in the dispersal group made five attempts to leave the disperser group. The first step of each attempt was the random selection of a territory. If the randomly selected territory contained no individuals, the individual

Table 5.4. Age distribution for population, disperser pool, and age-dependent probability of dispersal.

Age	Initial Population Distribution	Initial Disperser Pool Distribution	Probability of Dispersal
0	0.29	0.00	0.10
1	0.20	0.10	0.10
2	0.15	0.10	0.75
3	0.10	0.50	0.75
4	0.08	0.10	0.75
5	0.06	0.10	0.75
6	0.04	0.10	0.75
7	0.03	0.00	0.75
8	0.02	0.00	0.75
9	0.01	0.00	0.75
10	0.01	0.00	0.75
11	0.01	0.00	0.75

Table 5.5. Pack-size dependent probability of dispersers leaving a pack or joining a pack with an alpha of the same sex as disperser.

Pack Size	Probability of Leaving Pack*	Initial Joining a Pack with Same sex Alpha
1	0.00	0.00
2	0.00	0.25
3	0.10	0.75
4	0.10	0.75
5	0.50	0.75
6	0.80	0.75
7	0.80	0.50
8	0.80	0.50
9	0.90	0.25
10	0.90	0.25
11	0.90	0.05
12	0.90	0.05
13	0.99	0.00
14	0.99	0.00
15	0.99	0.00
16	0.99	0.00
17	0.99	0.00

*Calculated in model as a multiplier of age-dependent dispersal probability

Table 5.6. Fate of Dispersers in the Central Rocky Mountains, 1987 – 2000.

Wolf	Date Dispersed	Fate
Golgotha	November 1993	Left KNP
Magda	April 1997	Left BNP
Raven	June 1995	Left BNP
Peter	September 1992	Left PLPP
Pluie	Fall 1991	Left PLPP
Orion	November 1994	Left KNP
Snowy	October 1994	Remained in BNP
Nikita	December 2000	Left PLPP
Willow	March 2000	Left KNP
Aquila	April 1998	Left YNP
Betty	January 1992	Remained in BNP
Mariah	February 1999	Remained in BNP
Chinook	February 1999	Remained in BNP
Shadow	December 1993	Left KNP
Timber	March 1994	Remained in BNP
Merlin	October 1995	Left YNP
Ben	February 1995	Left BNP

moved into the territory with a probability of 1.0 and if the randomly selected territory contained only an individual(s) of the opposite sex, the individual entered this territory with a probability of 1.0. By this process an empty territory became a pack that was capable of reproduction. If the selected territory contained a breeding pair of individuals, then the dispersing individual was accepted into the pack with a probability that was pack-size dependent (Table 5.5). If the dispersing individual attempted to enter such a pack, but failed, then it died or dispersed from the population with a probability of 0.05.

If the individual was still alive after a failed attempt to become a member of a group, then it randomly selected another territory. One individual was permitted to attempt entering the same territory more than once within a single year. If an individual was alive after exhausting its attempts to leave the disperser group, then it remained a member of the disperser group until the next year of the simulation. I investigated the role of dispersers in population persistence by reducing the mean survival rate for dispersers and the proportion of dispersers in the population, and by increasing the probability of a disperser leaving the population.

Mating between mother and son and siblings occur rarely among wolves (Smith et al. 1997). This aspect of wolf biology was modeled in MORTA by selecting preferential replacement of an alpha by an immigrant. If the vacancy was not filled by the disperser group (e.g., if there is no dispersing wolf available to fill the vacancy), then a reproductively mature individual within the pack assumed the breeding role with a probability of 1.0. If at the end of this routine a pack is left without a dominant male and

Table 5.7 Parameter values for the simulation experiments, including parameter estimates and standard deviations. Relative sensitive analysis method was used to derive minimum and maximum values.

Parameter	Estimate		
	Minimum	Baseline	Maximum
Survival			
Pup survival	0.43	0.52	0.61
Pup survival sd	0.10	0.36	—
Pup survival without mother	0.10	0.3	0.5
Adult border survival	0.69	0.72	0.75
Adult border survival sd	0.05	0.16	0.25
Adult protected survival	0.84	0.89	0.94
Adult protected survival sd	0.05	0.19	0.25
Disperser survival	0.50	0.66	0.80
Reproduction			
Maximum litter size	4	8	10

Immigration/Emigration			
Number of immigrants	0	2	5
Probability of dispersing outside of population	0.02	0.10	0.20
Probability of dispersing for non-breeders	0.50	0.75	0.90
Proportion of dispersers in population	0.05	0.15	0.30
Density Dependence			
Population K	60	110	120
Population DD multiplier	0.50	0.77	0.90
Population DD shape factor	0.01	0.03	0.40
Pack K	12	20	25
Pack DD multiplier	0.50	0.77	0.90
Pack DD shape factor	0.01	0.03	0.40
Catastrophes			
Probability of catastrophe	0	0.01	0.1
Severity of catastrophe	0.5	—	0.2
Parvovirus	0.01	—	0.10

Temporal Variation in K			
Sinusoidal fluctuations in prey population	0.80 - 1.20	—	0.6 – 1.4
Exponential change in habitat	-0.005	—	0.005
Social Factors			
Probability of challenge	0.10	0.30	0.80
Probability of mortality with challenge	0.01	0.05	0.50
Probability pack splits if alphas die	0.10	0.40	0.75
Probability of joining a pack with same sex alpha	0.01	0.10	0.50
Probability of pack member filling alpha vacancy	0.50	1.0	—
Habitat Fragmentation			
Increased probability of dispersers leaving population	—	0.10	0.30
Reduced probability of finding vacant territory or pack	0.75	1.0	—

female, then each pack member leaves the territory and enters the disperser group with a probability of 0.4. This probability is consistent with observations from this study that a pack has a higher probability of splintering if an alpha animal dies. Packs that remain on territory without an alpha pair are unable to produce a litter until the alpha vacancy is filled. Changing status from being a territorial wolf to becoming a member of the disperser group was associated with an increased risk of mortality (Table 5.7).

Ascension

Occasionally, the alpha position and thus breeding rights is challenged by subdominant individuals within a wolf pack (Mech 1970; Zimen 1976). This phenomenon was modeled in MORTA by allowing for the potential of a dominant male or female to be evicted from its position of dominance by another individual. Data on the frequency of challenges made to the alphas by subordinates is non-existent for wild wolf populations. Consequently, I tested a number of estimates related to ascension before selecting parameters that resulted in model outcomes that were consistent with the observed dynamics of the population (Wiegand 1998). I assumed that an attempted takeover occurred every year within each pack with a probability of 0.40. The attempted takeover was initiated by a challenger that was the same sex as the current dominant individual. Recent immigrants into the pack received preference in being selected as a challenging wolf, and a challenger was selected at random from among the set of individuals that immigrated into that pack during the present year of the simulation. If the pack contained no individual that immigrated into the pack during that year, then a challenger was selected at random from among the individuals in that pack. An individual was eligible to be a challenger only if it was old enough to reproduce.

I assumed that the challenger successfully assumed the position of dominance with a probability of 0.30, that the loser of the challenge died with a probability of 0.05, dispersed from the pack with a probability of 0.40, or remained in the pack with a probability of 0.55. If the loser of the challenge dispersed, it was also exposed to the risk of mortality that is associated with any movement from a pack to the disperser group (Table 5.7). These probabilities are consistent with observations from this study that alpha animals tend to maintain their position of dominance for several years and intra-pack strife rarely results in the death of a wolf in the Central Rockies population.

Survival, Density Dependence, and Carrying Capacity

Because knowledge on density dependence in wolf populations is scarce (Peterson and Page 1988; Peterson et al. 1998), estimating the density-dependent function is difficult. MORTA (Vucetich et al. 2002) models density dependence through a modified value for survival that incorportes a density-dependent multiplier and a shape parameter that influences the strength of density dependence. Carrying capacity was modelled as the population size where survival is lowest rather than the equilibrium population size (Figure 5.2).

During each year of the simulation an individual survived with a probability that was age- and pack –specific (Table 5.7). I assumed the maximum age for a wolf was 11 years,

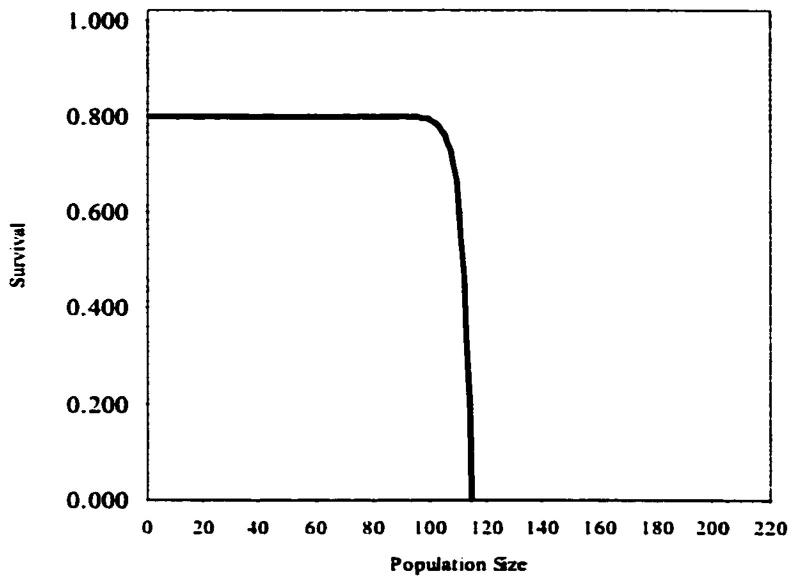

Figure 5.2. Density dependence function in survival.

which is consistent with data collected from the present study. The process of demographic stochasticity was simulated via a pseudo-random number generator to determine each individual's chance of survival. Environmental stochasticity was simulated by drawing a standard normal random variate each year. The random variate was transformed to reflect the mean survival rate and standard deviation in survival for each wolf, where the means and standard deviations are age- and pack- specific (Table 5.1). This transformed value represented a base value for survival (S_{base}) that is further modified by density-dependent factors.

MORTA models density dependence as the survival rate of each individual as a function of population size. An individual's annual probability of survival is:

$S = S_{base} \times S_{popdd} \times S_{packdd}$,

where S_{popdd} is the population-level density-dependent multiplier, S_{packdd} is the pack-level density-dependent multiplier.

The population-level density-dependent multiplier is given

by:

$$S_{popdd} = (1 - [1 - S_{Kpop}] [N / K_{pop}]^{1/Bpop})$$

where S_{Kpop} is the value of S_{popdd} when population size equals or exceeds the carrying capacity (K_{pop}), N is the population size, and B_{pop} is a shape parameter that influences the strength of density dependence. When $B_{pop} = 1$, the density-dependent function is linear. As B_{pop} decreases, density dependence becomes more curvilinear, and the effects on survival are delayed. The pack-level density-dependent multiplier is identical to the population-level density-dependent multiplier, and is given by:

$$S_{packdd} = (1 - [1 - S_{Kpack}] [N_{pack} / K_{pack}]^{1/Bpack})$$

where S_{Kpack} is the value of S_{packdd} when population size equals or exceeds the carrying capacity of the pack (K_{pack}), N_{pack} is the pack size during the current year, and B_{pack} is a shape parameter.

Peterson and Page (1988) observed a mean wolf survival rate of 0.43 during a population crash, which was precipitated by low moose densities. For the baseline model, I chose a shape parameter and a multiplier for the population and pack density-dependent function that conferred a higher survival rate (0.69 for protected pack members and 0.55 for border pack members) at K than that observed by Peterson and Page (1988) on Isle Royale because density-dependent effects may be more severe on Islands where little opportunity occurs for prey animals to immigrate into the population. Annual winter surveys of the wolf population in the Central Rockies suggests a current size of between 50 and 60 animals (Figure 5.3). I assumed the population K to be a maximum of 110 wolves, and the K of each pack to be 20 wolves.

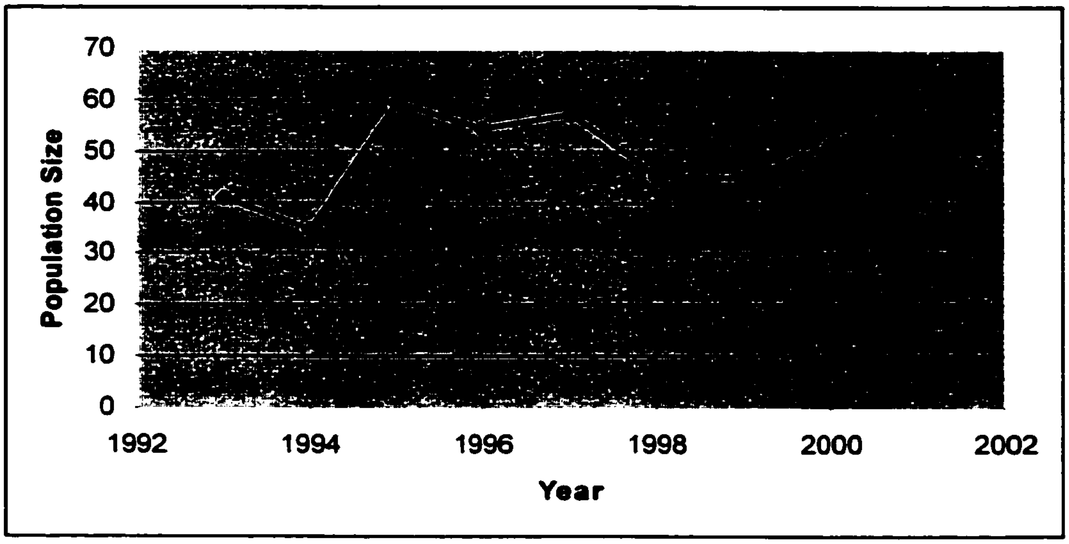

Figure 5.3. Wolf population size between 1993 and 2001, based on mid-winter ground tracking surveys over 18,670 km^2 of the Central Rocky Mountains.

Temporal Changes in Carrying Capacity

Environmental conditions that reduce carrying capacity or increase population growth rate variance decrease the probability of persistence (White 2000). Increased temporal variance also leads to lower persistence (Shaffer 1987).

Prey density and distribution is an important element of wolf population growth. Average wolf densities are strongly correlated with prey biomass per unit area (Keith 1983; Fuller 1989; Messier 1995). Because elk accounted for 68 % of the prey biomass consumed by wolves in the Central Rockies (Chapter 2), the density and spatial distribution of elk likely plays an important role in determining the wolf population K. Although data on elk density throughout the region is poor, current densities are approximately 0.04 elk/km^2 in the Bow Valley watershed of Banff National Park (Parks Canada unpublished data) and 0.25 elk/km^2 in the Kananaskis area (J. Jorgenson Alberta Department of Sustainable Resource Development, pers. comm.), 0.03 elk/km^2 in Kootenay National Park (Parks Canada unpublished data) and 1.0 – 1.5 elk/km^2 in provincial land adjacent to Yoho and Kootenay National Parks (B. Forbes B.C. Ministry of Environment pers. comm.). In most areas of the region, the elk population has declined and it is assumed that the area could support higher densities of elk (Parks Canada unpublished data; Raedeke and Raedeke 1998; J. Jorgenson Alberta Department of Sustainable Resource Development pers. comm.).

The present study has documented changes in territory sizes that coincide with a decline in prey over the past 7 years. The territory size of the Lougheed and Kootenay packs increased, the Bow and Spray packs amalgamated and continued to use both pack territories, and the Cascade pack killed the alpha female of the Panther pack and took over the Panther pack's territory while continuing to maintain most of their former territory (Paquet, Callaghan, and Hebblewhite unpublished data).

Although elk constitute an important part of wolf diet in the Central Rocky Mountains, the system also supports five additional prey species and very little information is known about the densities of species such as white-tailed deer and mule deer in the area. A low prey:predator ratio throughout the study area may explain the small litter and pack sizes, and large home range sizes. I modeled the effects of a fluctuating prey population on wolf persistence through a sinusoidal function of temporal variation in K.

Allee Effects

Small populations may experience low growth rate when the population is well below K because individuals experience difficulty in finding mates (Allee 1931). Although the model does not explicitly incorporate such 'Allee effects' in the density-dependent function, dispersing wolves must find mates in order to breed and reproduction will not occur unless a male and female of breeding age occupy a territory. Consequently reproduction may be reduced when the population is low.

Catastrophes

The structure of MORTA allows for a variety of environmental catastrophes to be modeled. I simulated the effects of canine parvovirus by decreasing pup survival to 0.25, with a probability of occurrence of 2% per year. In the baseline model, I simulated a catastrophe that caused survival for wolves of all ages to be 0.50, with a probability of occurrence of 1% per year. I investigated the sensitivity of the model to catastrophes by varying the probability of occurrence and the severity of a catastrophe. During a catastrophe year, individuals in all packs were exposed to the age-specific mortality rates, and mortality was not influenced by density-dependent effects.

Initial Age Distribution

I assumed an initial stable age distribution. Because age distribution data for the Central Rockies wolf population is poor, however, I set the initial distribution of each population by estimating an age distribution, running the simulation over 100 years, then using the final age distribution as the initial age distribution for a second simulation over 100 years. I then used the final age distribution in the model (Table 5.4).

Simulations

Several studies have highlighted the importance of testing PVA models to determine how accurately their projections reflect the behaviour of real populations (Brook et al. 2000; McCarthy et al. 2001). Moreover, Boyce (2001) recommended making predictions over a short time period due to variability inherent in population datasets. Consequently, I designed the first simulation to test the short-term predictive ability of the model by comparing results to actual population estimates between 1988 and 2001. The simulation was initiated with two wolves in each of 3 protected packs and 9 border packs. Extinction risk was defined as the mean proportion of extinctions out of 1,000 simulations over 16 years.

The second analysis was designed to investigate the relationship between population growth rate and various levels of adult mortality. The probability of extinction at year 10 was computed as the median of 1,000 simulations.

The third analysis was a sensitivity analysis to assess the role of survival, reproduction, immigration, emigration, density dependence, K, social factors, and catastrophes in population growth rate and population persistence (Table 5.2). I conducted this sensitivity analysis by varying each parameter while keeping all others constant at the baseline model values and examined the resultant population growth rate and risk of extinction. Where possible, a relative sensitivity analysis was applied (McCarthy et al. 1995; Cross and Beissinger 2001), whereby each parameter was adjusted by a fixed percentage relative to the range of each variable. The relative sensitivity analysis method allows for evaluation of the importance of each parameter within the bounds of the parameter's variability, or magnitude of potential change (Cross and Beissinger 2001). Extinction risk was defined as the median proportion of extinctions out of 1,000 simulations over 100 years.

The sensitivity analysis included investigating the effects of habitat fragmentation. The probability of a disperser colonizing a new pack or joining an existing pack with no alpha of the same sex was reduced from 1.0 to 0.75. I also increased the probability of a disperser leaving the population when it first disperses from its natal pack from 0.10 to 0.30.

The sensitivity analysis also investigated the effects of temporal variation in K on population persistence. The following scenarios were modeled in different simulations: 1) an increase in ungulate habitat due to a prescribed fire restoration program. This was modeled as an exponential increase in habitat at a rate of 0.5% per year for 15 years; 2) a decrease in ungulate habitat through habitat loss, modeled as an exponential loss in habitat at a rate of 0.5% per year for 15 years; 3) variation in the K of wolves due to fluctuations in the elk population, the primary prey of wolves in the Central Rockies (Paquet 1993). This was modeled as a sinusoidal curve, characterized by a maximum of 1.2 K, a minimum of 0.8 K, a 10-year periodicity of the cycle, starting with an increasing trend.

The fourth analysis was designed to estimate the number of protected packs required in a population of 12 packs with no immigrants, whereby the probability of extinction is less than 10% in 100 years. During each iteration of this analysis, the number of protected packs was increased by one and the number of border packs was decreased by one from the baseline model. The percentage of occupied packs of each pack type and probability of extinction at year 100 were computed as the median of 1,000 simulations. To investigate the interactions between the proportion of protected packs, immigration, and persistence, this analysis was also conducted with 0 – 5 immigrants per year.

RESULTS

The results of the first simulation show that the predictive ability of the model is relatively good. Most of the population count data from winter wolf surveys are within the bounds of the 5th and 95th percentiles of the simulation population, although prediction was poorer for years when the population consisted of only one or two colonizing packs (Figure 5.4).

Simulations to investigate population growth under various levels of adult mortality were consistent with data reported for wolf populations elsewhere (Fuller 1989; Figure 5.5). The number of initial packs in the population affected population growth. In simulations

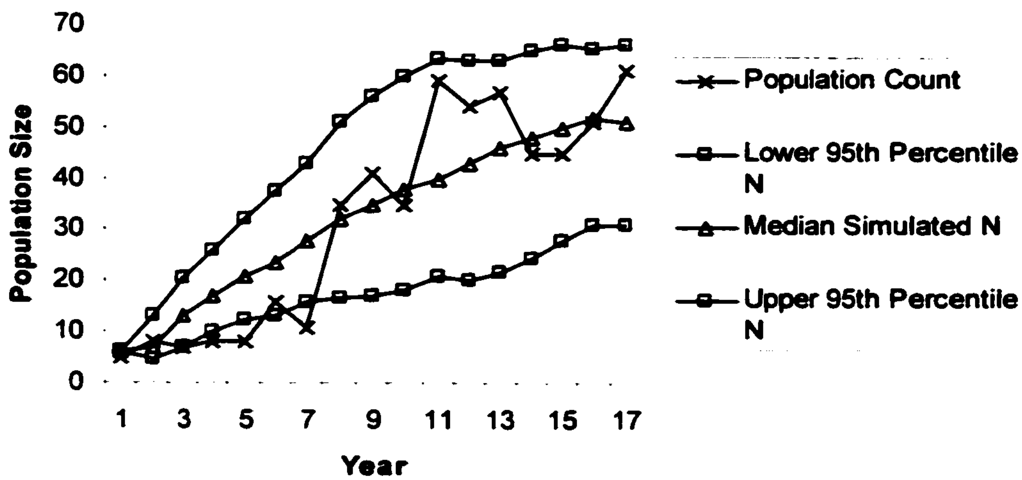

Figure 5.4. Annual population count data of the Central Rockies wolf population and the median population size of a simulated population. Upper and lower percentiles reported for the simulated population.

with 6 -12 initial packs (19 – 31 wolves), population growth was negative when the annual mortality was 30% or more; in simulations with 24 – 48 initial packs (55 – 103 wolves), population growth remained positive until annual mortality was 40% or more (Figure 5.6). The probability of extinction was also higher for packs with a low maximum number of packs than a population with a high maximum number of packs. For example, a population with an initial population of 4 packs and a maximum potential of 12 packs had a 0.53 probability of extinction when adult mortality was 30% per year, but a population with an initial population of 16 packs and a maximum of 48 packs had only a 0.01 probability of extinction in 10 years.

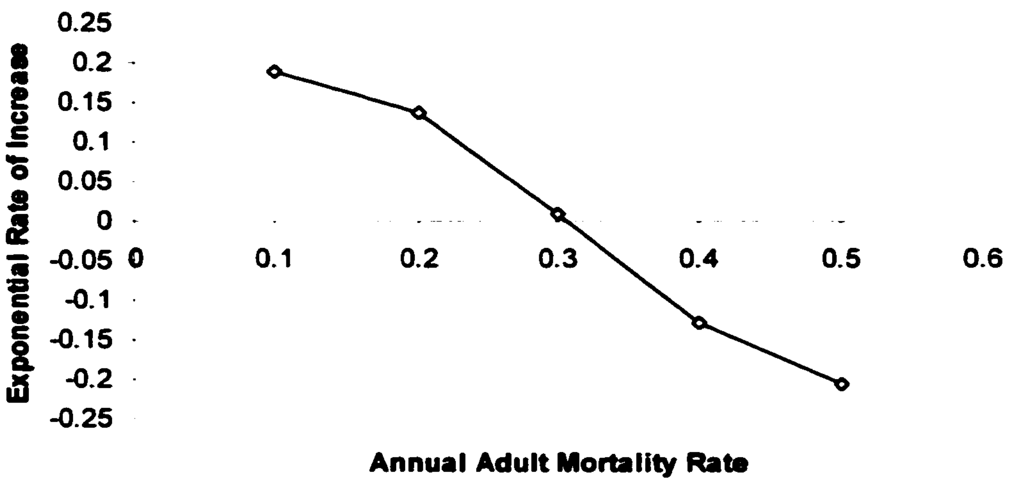

Figure 5.5. Relationship between population growth and annual mortality rate for adults in a simulated wolf population consisting of 16 territories.

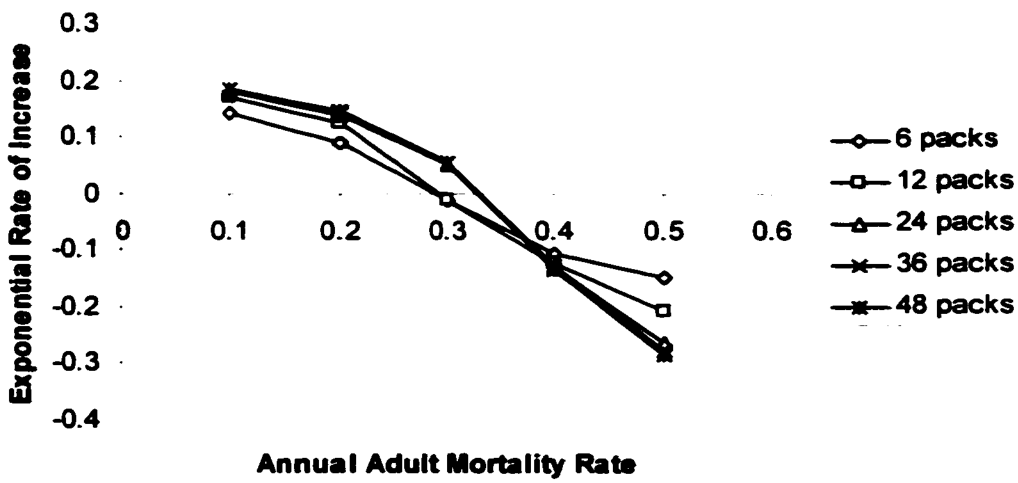

Figure 5.6. The effect of number of initial packs on population growth under various levels of adult mortality.

The proportion of occupied territories decreased with increasing levels of adult mortality (Figure 5.7). Populations with 10 - 20% annual mortality of adults maintained 100% occupancy of territories.

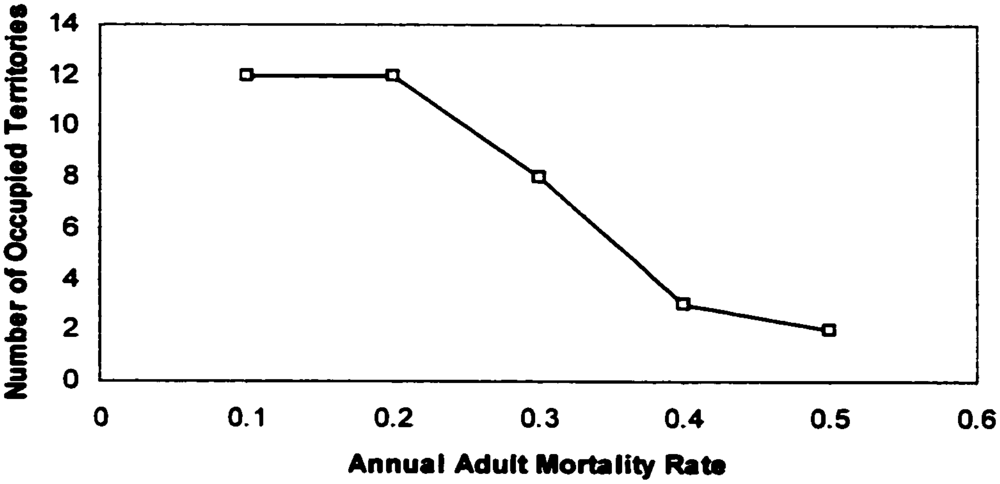

Figure 5.7. Relationship between annual mortality rate for adults and number of occupied territories in simulations with a maximum of 12 territories.

Simulations of the baseline model in the sensitivity analysis indicated that under current estimated conditions, the wolf population in the Central Rocky Mountains faces a low probability of extinction (0.07; Table 5.8). Baseline simulations also indicated that the median number of territories occupied remains below capacity (i.e. 10 of 12 territories occupied), which is consistent with data from recent population surveys.

Sensitivity analyses indicated that, under conditions of density dependence, the population K, number of immigrants, maximum litter size, and severity of catastrophe accounted for the greatest variability in the probability of extinction (Table 5.8). Density-independent simulations revealed that maximum litter size, number of immigrants, and the severity of catastrophes had the greatest effect on probability of extinction (Table 5.8). A reduction in the maximum litter size from 8 to 4 increased the probability of extinction by over 50%, and a reduction of immigrants to 0 per year increased the probability of extinction similarly by over 50% regardless of whether density dependence was incorporated in the model.

The least sensitive parameters to population persistence include disperser survival, proportion of dispersers in the population, the standard deviation of survival, the probability of a challenge for alpha position, a reduced probability of finding a vacant pack or territory, and the probability of pack members leaving the pack if the alphas die. Pack density-dependent factors were less important to population persistence than the population density-dependent factors (Table 5.8).

Several simulations resulted in the occupation of fewer territories than under baseline conditions (Table 5.9). The greatest reduction in the number of occupied territories occurred under conditions of severe density dependence at the population or pack level, 0 immigrants per year, a low population K, or an exponential decrease in population K. Alternatively, a high population K, a large number of immigrants per year, and more than 7 protected packs in the system resulted in a higher numbers of occupied territories than under baseline conditions. Under most conditions, protected packs retained the full compliment of three territories.

The fourth simulation indicated that, in the absence of immigration, 9 protected packs of 12 would be required to maintain a population of wolves in the study area with a probability of extinction that is less than 10% (Figure 5.8). The probability of extinction declined dramatically in simulations where the number of protected packs was increased from 3 to 7. The area required to maintain a viable population of wolves in the Central Rockies in the absence of immigration is approximately 14,600 km^2 (Figure 5.9), and includes current protected areas (totalling 11,130 km^2) as well as areas that are currently under provincial jurisdiction and governed by liberal wolf hunting and trapping regulations.

The number of immigrants affected the probability of extinction significantly, especially for simulations in which 0 – 6 packs were protected (Figure 5.10). For simulations in which more than 6 packs were protected, the high survival rate of adults allowed for dispersers to colonize vacant territories or join packs with no alpha of the same sex, and reproduce, thus reducing the probability of extinction. Simulations with 12 protected packs resulted in a low probability of extinction (3.3%) even with 0 immigrants.

Table 5.8. Sensitivity analysis of the stochastic wolf PVA model run in MORTA indicating proportion of change in probability of extinction due to a change in parameter value.

	Density Dependent	Density Dependent	Density Independent	Density Independent
Parameter	Low Estimate Change	High Estimate Change	Low Estimate Change	High Estimate Change
Survival				
Pup survival	-0.09	0.045	-0.07	0.01
Pup survival without mother	-0.03	0.045	-0.07	-0.02
Adult border survival	-0.07	0.046	-0.06	0.01
Adult protected survival	-0.02	0.043	-0.03	0.01
Adult border and protected survival	-0.16	0.057	-0.14	0.02
Pup survival sd	0.039	___	-0.03	___
Adult border sd	0.03	-0.029	0.003	-0.03
Adult protected sd	0.019	0.008	0.01	0.002
Adult border and protected sd	0.01	-0.032	0.01	-0.02

Reproduction				
Maximum litter size	-0.54	0.057	-0.589	0.01
Immigration/Emigration				
Number of immigrants	-0.61	0.069	-0.49	0.02
Probability of dispersing outside of population	0.04	-0.13	0.01	-0.03
Probability of dispersing for non-breeders	0.01	0.04	-0.01	-0.001
Proportion of dispersers in population	0.01	0.03	___	___
Disperser survival	0.00	0.04	-0.02	0.004
Density Dependence				
Population K	-0.67	0.03	___	___
Population DD multiplier	0.04	-0.16	___	___
Population DD shape factor	0.01	-0.33	___	___
Population DD multiplier and shape factor	0.05		___	___
Pack K	-0.09	0.02	___	___
Pack DD multiplier	0.03	0.02	___	___

Pack DD shape factor	0.02	-0.10	___	___
Population DI and pack DD low	0.05	___	___	___
Catastrophes				
Probability of catastrophe	0	-0.42	0	-0.32
Severity of catastrophe	0.04	-0.39	0.01	-0.35
Parvovirus	0.04	-0.01	0.01	-0.03
Temporal Variation in K				
Fluctuations in prey population	-0.02	-0.35	___	___
Exponential increase in habitat	0.05	___	___	___
Exponential decline in habitat	0.03	___	___	___
Social Factors				
Probability of challenge	0.01	0.01	0.01	-0.001
Probability of mortality with challenge	0.03	-0.07	0.01	-0.07
Probability pack splits if alphas die	0.02	0.01	0.002	-0.01

Probability of joining a pack with same sex alpha	0.02	0.00	0.01	-0.02
Probability of pack member filling alpha vacancy	-0.08	___	-0.04	___
Habitat Fragmentation				
Increased probability of dispersers leaving population	-0.14	___	0.002	___
Reduced probability of finding vacant territory or pack	-0.02	___	-0.01	___

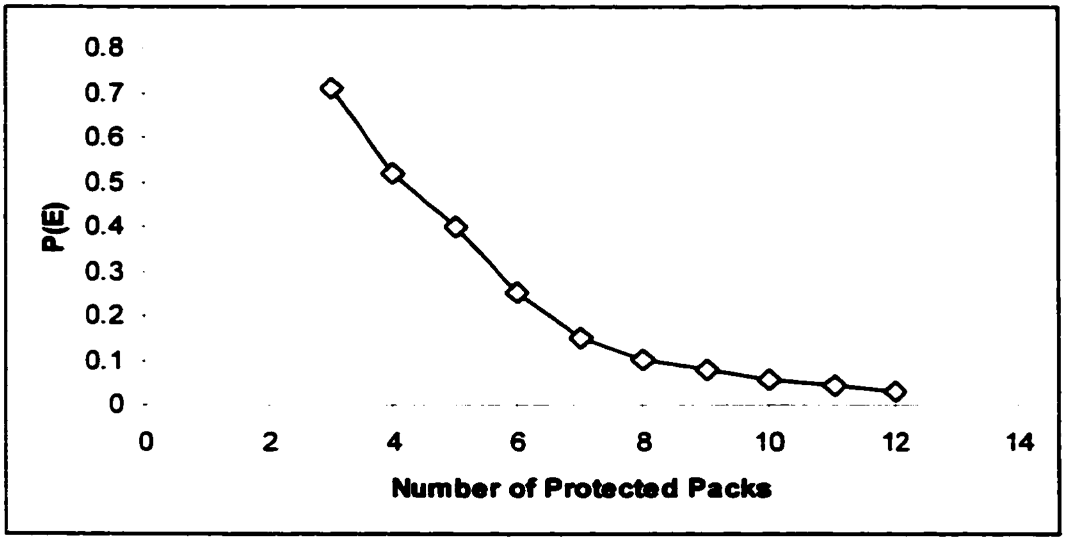

Figure 5.8. Relationship between number of protected packs of 12 in the study area and probability of extinction in the absence of immigration.

Table 5.9. Sensitivity analysis of the stochastic wolf PVA model run in MORTA indicating median number of viable packs resulting from a change in parameter value.

Parameter	Number of Viable Packs			
	Density Dependent Low Estimate	Density Dependent High Estimate	Density Independent Low Estimate	Density Independent High Estimate
Baseline Model	10	—	11	—
Survival				
Pup survival	9	10	10	12
Pup survival without mother	10	10	11	11
Adult border survival	9	10	11	12
Adult protected survival	10	10	11	12
Adult border and protected survival	9	10	10	12
Pup survival sd	10	—	11	—
Adult border sd	10	9	11	11
Adult protected sd	10	10	12	11
Adult border and protected sd	10	9	12	11

Reproduction				
Maximum litter size	8	10	8	12
Immigration/ Emigration				
Number of immigrants	8	11	10	12
Probability of dispersing outside of population	10	10	12	11
Probability of dispersing for non-breeders	9	10	11	11
Proportion of dispersers in population	10	10	___	___
Disperser survival	10	10	11	11
Density Dependence				
Population K	5	10	___	___
Population DD multiplier	8	10	___	___

Population DD shape factor	10	10	___	___
Population DD multiplier and shape factor	11	7	___	___
Pack K	9	___	___	___
Pack DD multiplier	10	10	___	___
Pack DD shape factor	10	9	___	___
Population DI and pack DD low	11	___	___	___
Catastrophes				
Probability of catastrophe	10	9	11	10
Severity of catastrophe	10	10	11	11
Parvovirus	10	10	11	11

Temporal Variation in K				
Fluctuations in prey population	9	8	___	___
Exponential increase in habitat	11	___	___	___
Exponential decline in habitat	9	___	___	___
Social Factors				
Probability of challenge	10	10	11	11
Probability of mortality with challenge	10	9	11	10
Probability pack splits if alphas die	10	10	11	11
Probability of joining a pack with same sex alpha	9	9	11	11
Probability of pack member filling alpha vacancy	9	___	11	___

Habitat Fragmentation				
Increased probability of dispersers leaving population	9	___	10	___
Reduced probability of finding vacant territory or pack	9	___	11	___

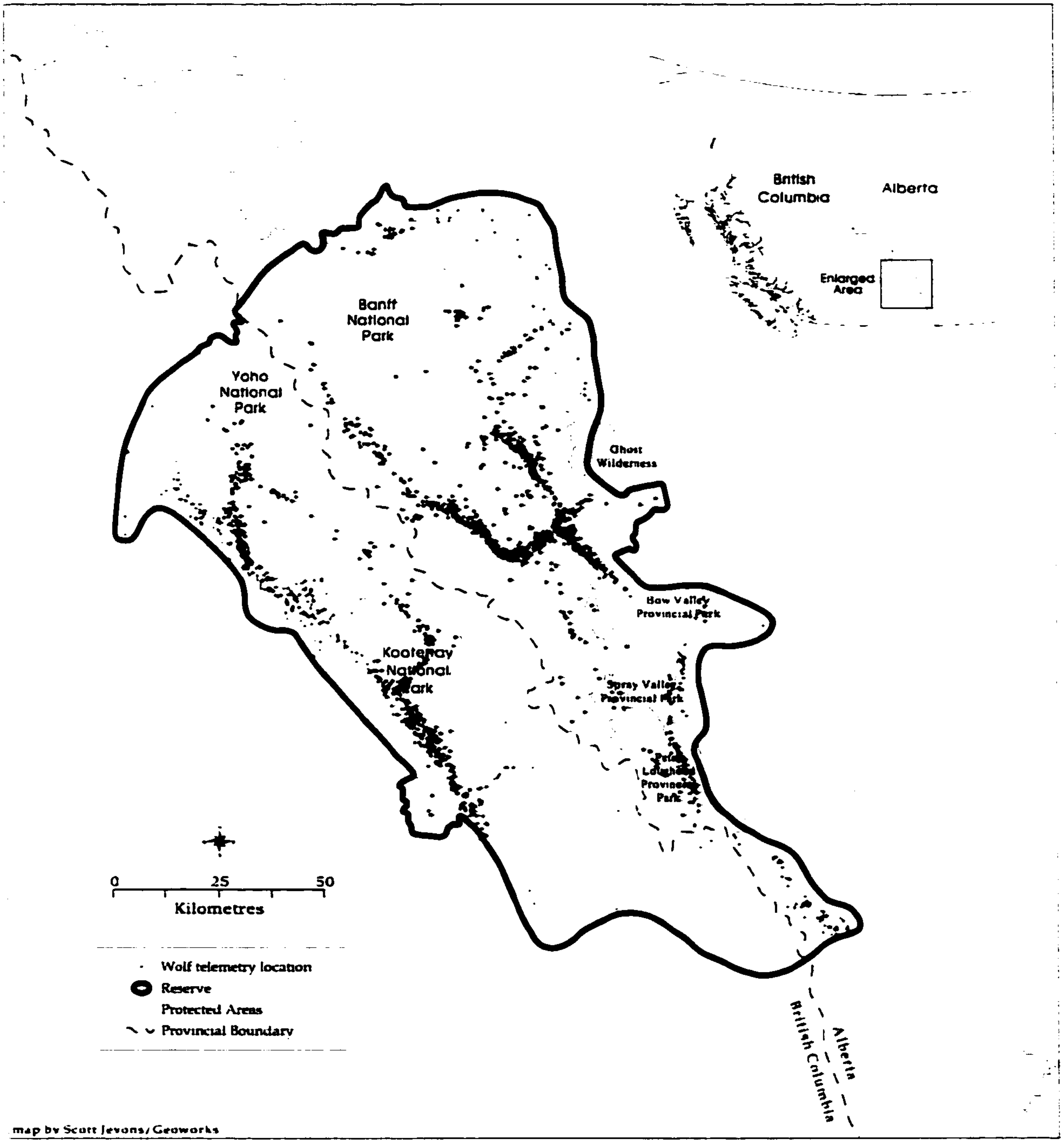

Figure 5.9. 14,600 km² area required to maintain a viable population of wolves without immigrants in the Central Rockies.

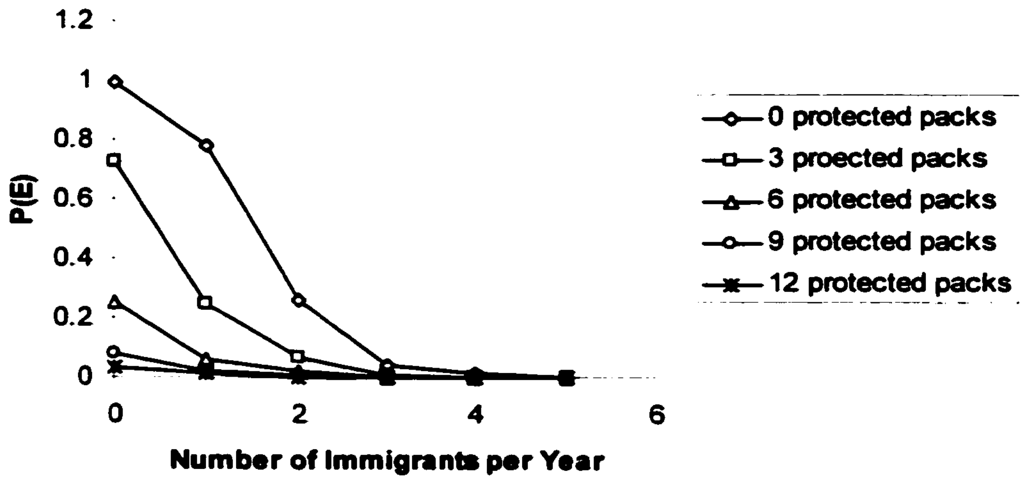

Figure 5.10. Relationship between number of protected packs, number of immigrants per year, and extinction risk.

DISCUSSION

The results of the simulations do not provide a definitive prognosis for the wolf population occupying the Central Rockies. Stochastic PVA models are designed to estimate population trends given the mean population parameters and stochastic elements (Lacy and Clark 1990). Simulation models enhance our understanding of the processes that influence population dynamics, and are useful for evaluating the consequences of alternative management actions by feeding into an iterative cycle of adaptive management and modeling (Walters 1986; Boyce 1994). Moreover, the modeling process allows for the development and testing of competing hypotheses about the dynamics of the system that will help improve our understanding of the risks faced by a population and focus management priorities (Boyce 2001).

Assumptions were made in the modeling process about density dependence, including the shape and multiplier of the density-dependent function. Estimating density-dependent relationships is very difficult (Ginzburg et al. 1990) and choosing an adequate time scale to estimate density dependence is critical to avoid making erroneous assumptions on the behaviour of populations over a small window of time (McCullough 1990). Few studies have focused on recording density-dependent effects on wolf populations (Peterson and Page 1988; Peterson et al. 1998) and most wolf populations have been studied over a time scale inappropriate for testing density dependence. Boyce (1992) suggested treating a density-dependent model as the null model in a hypothesis-testing framework.

The assumption that K=110 wolves also affected the outcome of the model. Although a high mortality rate and reduced productivity, which are indicative of a population reaching K, have not been documented in the Central Rockies wolf population, a K of less than 110 (e.g. 80-90 individuals) may be more realistic given the habitat constraints imposed on the population. Using a K of 110 individuals resulted, however, in population trajectories that are consistent with the current understanding of the population dynamics. Choosing parameter values that reflect the observed dynamics of the system is one method to deal with uncertainty in PVA due to lack of data for specific model parameters (Wiegand 1998; Boyce 2001).

Despite intensive field studies on wolves in the Central Rockies, some of the model parameter estimates were based on limited information. Knowledge of immigration and age-dependent and pack-size dependent dispersal behaviour is weak, as is knowledge of frequency of challenges to dominance and ascension and survival rate of dispersers. Because the least sensitive parameters to population persistence include disperser survival, proportion of dispersers in the population, dispersal behaviour, and the probability of a challenge for alpha position, greater knowledge of these parameters may not lead to a greater understanding of wolf population dynamics. Knowledge of litter size distribution in the Central Rockies wolf population is sufficient, however, and this parameter is one of the most relevant to population persistence.

Pack density-dependent factors were less important to population persistence than the population density-dependent factors (Table 5.8). This result indicates that a management focus on increasing the number of protected packs in the region will have greater influence on population persistence than increasing the number of individual wolves and is consistent with the results of Vucetich et al. (1997).

The Central Rockies wolf population is comprised of subpopulations (packs) with differential mortality. The difference in mortality rate is due primarily to deterministic anthropogenic effects (edge effects) in areas adjacent to protected reserves. Packs bordering on protected reserves and non-protected areas are exposed to a higher risk of human-caused mortality than wolves occupying protected areas. The implications of edge effects for the population are a low equilibrium population size, a reduced number of occupied territories, and a reliance on immigrants for population persistence. A low equilibrium population size results in greater vulnerability to stochastic effects (Gilpin and Soulé 1986; Shaffer 1988), and stochastic effects may be magnified for socially breeding species with a small number of breeding groups (Vucetich et al. 1997). Haight et al. (1998) similarly concluded that a fragmented population of wolves occupying lower quality habitat can remain viable provided immigration offsets wolf mortality.

In addition to anthropogenic effects, the prey habitat in the protected reserves is more topographically complex and consequently less productive than areas adjacent to the mountainous reserves (Carroll et al. 2000). The topographical makeup of the protected areas likely poses limitations to the carrying capacity of the wolf population by limiting the population density of prey species. Small litter sizes and relatively small pack sizes may be the result of low prey: predator ratios. Complex topography and the resultant low prey: predator ratio in the protected reserves may be a contributing factor to wolf use of the less topographically complex landscape adjacent to the protected reserves, where prey density is higher but human-caused wolf mortality is also higher (Chapter 3). Pack territories are larger in the Central Rockies than in areas that are relatively homogeneous (e.g. deciduous or boreal forests), which reduces the maximum reproductive potential of the population. Moreover, the low number of territories available in the region reduces the opportunity for dispersers to select territories with lower risk of human-caused mortality. Data from the present study show that most (71%) of known dispersers left the population, which may be a further consequence of limited territory options within the region.

The combined effects of topography and edge effects compromise the viability of the Central Rockies wolf population. The protected areas provide for the full home range of only 2-3 packs of 12 in the region. Although under current conditions extinction is not imminent, the reliance of the population on immigrants from the non-protected areas outside of the reserves suggests that a cautious approach should be taken to avoid increased edge effects that reduce the viability of the population. Vucetich and Paquet (2000) proposed that a population occupying a protected area should not be considered viable if it relies on surrounding unprotected populations of wolves to prevent the extinction of the protected population.

The discussion of protected areas functioning as baselines for measuring ecological change is contemporaneous in conservation biology (Janzen 1983; Schonewald-Cox 1988; Arcese and Sinclair 1997; Sinclair 1998). Sinclair (1998) suggests that protected areas should be expanded to fulfill their role as ecological baselines. The minimum area required to maintain a wolf population in the Central Rockies with a low probability of extinction in the absence of immigration from unprotected populations is 14,600 km^2, which exceeds the combined current size of the protected areas (11,130 km^2) in the study area by 4,441 km^2. This estimate of the minimum area required to maintain a population of wolves exceeds estimates determined with less detailed information on movement patterns and viability analyses (Burkey 1995; Schonewald-Cox et al. 1988; Gurd et al. 2001; Landry et al. 2001). Burkey's (1995) estimate, which was most similar (12,000 km^2) to the present study, pertained to national parks in western North America, where mountainous habitat exists.

If the minimum area required to maintain a protected population exceeds the size of the protected area, then a provision to expand the protected area is prudent (Landry et al. 2001). Alternatively, inter-jurisdictional human-use management, whereby human-caused mortality of wolves adjacent to protected reserves is reduced or eliminated, may achieve results similar to expanding the existing protected areas. Regardless of the strategy applied, a biologically based approach is necessary to redress the mismatch between the scale of management actions and the scale of the ecological response (Ruggiero et al. 1994).

Immigration is an important element in the viability of the Central Rockies wolf population, and maintenance of the number and capability of immigrants to move into the population will likely contribute to the long-term persistence of the population. Unanticipated changes in management focus in provincial lands may, however, reduce the number of dispersers immigrating into the population. For example, wildlife managers in the East Kootenay district, adjacent to Kootenay and Yoho National Parks, placed emphasis recently on reducing predator numbers through increased trapper and hunter efforts. Consequently, hunter - and trapper -caused wolf mortalities increased by two-fold during the 2000/01 hunting and trapping seasons from that of previous years (British Columbia Ministry of Environment unpublished data).

Wolf productivity depends on the availability of ungulates (Zimen 1976; Keith 1983; Messier 1985; Fuller 1989; Boertje and Stephenson 1992). The mean litter size was lower in this study (4.0 +/- 2.1 SD) than areas where ungulate density was high (Harrington et al. 1983; Fuller 1989; Boertje and Stephenson 1992; Hayes and Harestad 2000), and was on the lowest end of the range (4.0 – 7.0) reported by Fuller (1989). The low productivity suggests that the prey density and thus carrying capacity for wolves in the Central Rockies is likely lower than in other areas. This may also offer an explanation as to why productivity did not fully compensate for the higher mortality rate in border packs. Average wolf densities are strongly correlated with prey biomass per unit area (Keith 1983; Fuller 1989; Messier 1995). The viability of a wolf population is likely limited by prey density (Vucetich and Paquet 2000; Fuller and Sievert 2001). A decrease in prey density reduces carrying capacity and increases the variance in population growth rate. With a concomitant decline in prey density across the region, the territory size of several packs increased. These observations are consistent with other studies that documented behavioural changes such as increased territory size or intraspecific strife following a decline in prey abundance (Mech 1977; Peterson and Page 1988; Peterson et al. 1998).

Recent management efforts in the Bow Valley of Banff National Park, where the territories of 2 protected packs in the population exist, have focused on reducing the number of elk surrounding the town of Banff. Two hundred and seventeen elk were removed from the town and surrounding areas between 1998 and 2001, and predators, automobile and train collisions reduced the prey population elsewhere in the Bow Valley over the past decade. The 2001 spring aerial elk survey estimated 277 elk in the Bow Valley, which is 27% of the 1989 spring aerial survey estimate of 1011 elk (Parks Canada unpublished data). If the current elk population is not high enough to sustain 2 wolf packs and a cougar population, local wolf productivity may decrease and dispersal and mortality may increase, reducing the overall viability of the Central Rockies wolf population.

Thorough evaluations of models require rigorous research and adaptive management (Boyce et al. 1994). Predator populations are sustained by prey population productivity rates (Carbone and Gittleman 2002). Assessing prey density and distribution and their demographic effects on carnivore populations are thus important for predicting the potential for population persistence (Fuller and Sievert 2001). Estimates of prey population productivity rates are currently unavailable for most of the Central Rockies. Studies on elk population dynamics in the East Slopes of the Central Rockies were initiated recently, however, and such research will improve the predictability of the current model. Gathering information on future plans for building roads in provincial lands adjacent to the protected reserves will also help to predict changes in human-caused mortality. This research also highlights the need for monitoring the rate of immigration into the protected areas of the Central Rockies and to understand the mechanisms responsible for the variation in dispersal and immigration.

Dispersal behaviour and social organization have important consequences for population persistence of social carnivores such as wolves. The effects of such behaviours on persistence may be magnified in mountainous habitats including the Central Rockies where home ranges are large and consequently few packs exist. Moreover, the ranging behaviour of wolves and the topographical complexity of the region increase edge effects in the Central Rockies by exposing wolves to risks of mortality along the borders of protected reserves. Landscape-level management of human activities may be required to ensure the persistence of the Central Rockies wolf population.

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CHAPTER 6

GENERAL DISCUSSION

The Connection Between Topographical Complexity, Habitat Use, Survival, and Persistence

The results in Chapter 2 and 4 provide strong evidence that topographical and climatic factors restrict wolf movements to low elevation areas during the winter in mountainous habitats such as the Central Rocky Mountains. These results are consistent with Green (1951:24):

> The ideal habitat of the wolf of western Canada is comparatively flat, open, and semi-open country where its characteristic cursory hunting technique can be employed to the necessary advantage. Due to the extreme mountainous nature of park terrain, suitable habitat is more or less confined to isolated areas of the required topographic character, a circumstance which not only limits occurrence but also extension of range. Wolf activity, therefore, is largely restricted to the broad river valleys and neighbouring slopes and passes.

Topographical complexity not only influences wolf activity, but also affects human activities. Human infrastructure such as roads and trails, for example, are most abundant in the broad river valleys that Green (1951) described. Such modifications of the landscape allow wolves to move more efficiently, especially in winter, as well as restrict wolf movements through areas of high human activity. The convergence of wolf and human activities during winter creates a tension between repulsion from and attraction to habitats that has positive and negative effects on wolves, and also has the potential to affect predator-prey dynamics. Roads in particular both enhance and restrict wolf movements, and road traffic is a source of wolf mortality, although population effects of traffic collisions were not detected.

The disparate results related to wolf mortality and traffic volume in Chapter 3 and 4 merit some discussion. The multivariate analysis of factors related to wolf mortality in Chapter 3 suggests that traffic volume does not have a strong influence on wolf survival; alternatively, the results of Chapter 4 suggest that high traffic volume is associated with more wolf deaths than low to moderate traffic volume. The multivariate analysis on wolf survival used a relatively small sample of wolves (31), 3 of which were killed on roads. A larger sample may have helped to elucidate better the relationship between wolf survival and traffic volume. The traffic-volume - wolf death relationship presented in Chapter 4 may be considered unrepresentative of mortality risks experienced by the population because it does not use a radiocollared sample. A sample of wolves killed by automobile collisions, radiocollared or not, however, is appropriate for addressing questions regarding the relationship between traffic volume and wolf mortality.

The implications of habitat use restrictions imposed by the topographical complexity of mountain systems and the attraction of wolves to compacted roads and trails may include increased exposure of wolves to hunting and trapping pressure. Mech (1977:559) indicated that "human-caused mortality of wolves ... is greatly influenced by accessibility." A fall and winter convergence of wolves and elk occurs in low elevations adjacent to the protected areas in the Central Rockies due to deep snow at higher elevations. This convergence may increase hunter and trapper accessibility to wolves.

Moreover, road placement occurs in the lowest elevations, and wolf use of roads with low to moderate traffic volume as efficient travel routes may increase the probability that hunters or trappers will encounter wolves.

Another important aspect of the interplay between topographical complexity and wolf habitat use is the resultant occupation of large territories by wolf packs. Average home range for wolf packs in the Central Rockies is 1,709 km^2. Home ranges in less topographically complex terrain areas range from 116 km^2 (Fuller 1989) to 1,250 km^2 (Oosenbrug and Carbyn 1985). Fritts and Carbyn (1995:26) postulated that "... the ability of existing nature reserves to support viable wolf populations appears related to a variety of *in situ* circumstances, including size, shape, and topography...." Topographical complexity is an example of "environmental conditions that reduce carrying capacity or increase variance in the growth rates of populations [thus] decrease persistence probabilities" (White 2000:291). Rugged terrain limits prey availability, which affects the carrying capacity of wolf populations occupying such habitats, and consequently reduces the ability of existing protected reserves to support a viable population of wolves. The result of topographical restrictions in the Central Rockies is one of the lowest recorded wolf densities in the world.

High rates of emigration may also be a consequence of topographical complexity. Where territories are large, fewer territories exist in a population and dispersers have reduced opportunities to find a vacant territory, which may result in a larger proportion of dispersers leaving the population. Hayes and Harestad (2000) recorded numerous cases of dispersers establishing a territory adjacent to their natal territory during the colonisation period of a wolf population in the Yukon. This behaviour resulted in a low proportion of dispersers leaving the population and a higher population growth rate. In contrast, most (71%) radiocollared emigrants from the present study dispersed beyond the protected areas.

The balance of evidence from this thesis supports the view that anthropogenic effects are a serious challenge to the conservation of large carnivores such as wolves (Weaver et al. 1996; Woodroffe 2001). This thesis shows that, in the absence of immigration from surrounding unprotected lands, hunting and trapping on the edge of protected reserves reduces the persistence of wolves in the protected areas of the Central Rockies. Moreover, a current management directive to reduce elk densities within the Bow watershed of Banff National Park may negatively affect regional wolf population persistence by reducing the number of protected packs and causing border packs to spend more time in unprotected areas where they are exposed to hunters and trappers.

Weaver et al. (1996) characterized wolves as the large carnivore species with the greatest level of resilience to anthropogenic effects in the Rocky Mountains. This conclusion was based on dispersal behaviour and life history traits such as productivity and dispersal ability but the analysis did not consider the limitations imposed on such resilience by topographical complexity of the Rocky Mountain ecosystem. Of the four carnivores discussed by Weaver et al. (1996) (grizzly bear [*Ursus arctos*], cougar [*Felis concolor*], wolverine [*Gulo gulo*] and wolf), only the wolf has been extirpated historically from the

Central Rockies. This extirpation was caused by overexploitation by humans and low prey densities (Paquet 1993). Moreover, although brown bear (*Ursus arctos*) and cougar populations disappeared before wolf populations in relatively homogeneous terrain in North America and Europe, wolves were extirpated prior to bears and cougars in mountainous habitat in Europe and North America (Woodroffe 2001). Habitat use restrictions, convergence of humans, prey, and wolves during fall and winter, use of roads and trails by wolves as efficient travel routes, and the extensive ranging behaviour of wolves in the Central Rockies are all influenced by the topographical complexity of the region.

Conflicts with humans on unprotected land next to reserves in the Central Rockies region reduced the probability of persistence of the wolf population. Woodroffe and Ginsberg (1998) investigated anthropogenic effects on large carnivores by comparing their persistence in reserves of varying sizes and concluded that the magnitude of edge effects is greater for small reserves because fewer home ranges are fully contained within the bounds of the reserve. Mountainous habitat may similarly magnify edge effects for wide-ranging carnivores such as wolves, however. The topographical complexity of the area reduces prey density, which consequently increases home range sizes of wolf packs and creates a low perimeter:area ratio. A lower perimeter:area ratio in the protected areas exposes wildlife populations within the reserves to the effects of adjoining habitat (Buechner 1987). Even a relatively large reserve such as Banff National Park (6,641 km^2) fully protects only 1 wolf pack of 6 occupying the park. A second pack is now fully protected from hunting and trapping due to the designation in 2001 of a provincial park in

Alberta adjacent to Banff National Park. The newly designated provincial park includes the portion of this pack's territory on provincial land and where wolf hunting was permitted prior to the designation of the provincial park.

Topographical complexity in the Central Rockies limits wolf population size and human-caused mortality reduces survivorship. My data show that, in the absence of immigration from surrounding unprotected lands, the combined effects of topographical complexity and human-caused mortality increase the risk of population extinction. This surprising result is contrary to Woodroffe's (2001:69) conclusion that "carnivore populations may be unable to persist on the edges of reserves unless they are continually replenished by immigrants from the *safer reserve core*" [emphasis added]. Woodroffe assumed that protected areas provide immigrants to offset the effects of higher rates of mortality in areas bordering reserves, but this thesis provides evidence to the contrary: the Central Rockies wolf population relies on immigrants from the *unprotected areas* of the region to maintain population viability within the protected areas.

The rate of mortality in border packs in and of itself does not project imminent extinction of the population, provided a minimum of 2 immigrants per year enter the population from surrounding unprotected lands. Thus, if current conditions in the unprotected lands beyond the population prevail, whereby a source of immigrants is maintained, there may be no need to extend the boundaries of the protected areas, as was suggested in Chapter 5. If anthropogenic activities such as road development and associated hunting or trapping activities increase, however, population persistence might be reduced. Fritts and Carbyn

(1995:26) caution that protected reserves "are the most secure places ... to which the [wolf] range could collapse in future decades or centuries, facilitated by habitat fragmentation..." Although the combined protected areas in the Central Rockies total 10,159 km^2, they are ineffective to support a viable wolf population without relying on immigrants from beyond the protected areas. Thus, if wolf range in the Central Rockies collapses to protected reserves in the future, population viability is unlikely.

Conservation Implications

Two obvious conservation tactics that focus on reducing edge effects on the wolf population come to the fore. The first one deals with the possibility of establishing a protected area system that is capable of meeting the ecological needs of the wolf population. Opinions on the best method(s) of establishing adequate protected areas vary. Weaver et al. (1996:972), for example, suggested: "with their productivity and dispersal capability, wolves ... might respond sufficiently to refugia that are well distributed in several units across the landscape at distances scaled to successful dispersal." Successful conservation planning for wolves in the Rocky Mountains must do more, however, than establish refugia across broad scales. A scattering of small reserves across the region would do little to protect a wolf population in the Rocky Mountains due to the wide-ranging behaviour of wolves and the associated overlap of territories between protected and non-protected areas. Alternatively, Woodroffe (2001:91) proposed: "planning of protected area networks must therefore consider the densities and ranging behaviours of all species to be protected". This thesis provides insight into the level of information required to inject into the conservation planning process, such as the range of movements by wolves occupying protected reserves.

Sinclair (1998) described an ideal scenario whereby society is willing to set aside their desires to benefit from land use for consumptive recreational and resource extraction purposes in favour of ensuring ecosystem integrity in selected areas in perpetuity:

> Irrespective of their historical origins and in absence of suitably large alternative areas, protected areas have become baselines for measuring ecological change...Ecological baseline areas must necessarily be large enough to represent natural habitats and natural ecosystem dynamics. It is unlikely that any area is now completely free of human impacts, but baselines must be relatively free of direct impact at present and in the future...This function for parks is so urgent that it supersedes any other historical roles that these areas may have had... The larger the baseline area the more likely it will represent relatively undisturbed processes; national parks should be expanded as much as possible to meet this requirement (Sinclair 1998, pp. 399-400).

Given the nature of human enterprise, however, it is unlikely that an additional 4,441 km^2 of land will be set aside as a protected reserve in the Central Rockies (see Figure 5.9). It is perhaps more realistic to expect a cooperative management effort between national parks, provincial parks, and non-protected lands. The second conservation tactic would thus focus on establishing wolf hunting and trapping exclusion zones adjacent to the protected areas, which would have an equally beneficial effect on population persistence as establishing larger reserves.

In referring to developing large carnivore conservation strategies in the Rocky Mountains, Weaver et al. (1996:965) emphasized that successful strategies "will have to incorporate scientific knowledge of how these species persist in the face of different disturbances". Such knowledge is as important to an effective wolf conservation strategy as it is to a large carnivore conservation strategy.

Conservation must not only rely on science, however, and history has shown that science is only one element in a gestalt of factors that culminate in policy formation, a critical component of conservation. Perhaps the most important role of scientists in the policy process is in "diagnosing emerging problems or in providing a foundation for the integrated understanding of the need for policy design" (Holling 1995:5). Expounding on Holling's idea, Paquet (1999:oral presentation) emphasized: "scientific knowledge provides the sideboards that constrain discussions about human use and policy in carnivore conservation." Where carnivores are allowed to persist, such as within and adjacent to protected reserves in the Central Rockies, scientific knowledge of the ecological needs of carnivores should provide the framework for management discussions.

A coordinated approach to wolf persistence across multiple jurisdictions brings its own unique challenges that are largely social. Clark et al. (1996:946) describe some of these challenges inherent in carnivore conservation that are also applicable to wolf conservation:

> ...most ecosystems large enough to support large carnivores are managed by several different [agencies] ... as well as myriad private land owners. Each agency operates under different legislative mandates, histories, and standard operating procedures, which limits or precludes exchange of information and expertise, open communication, joint decision-making, and others mechanisms required for true cooperation at macro-system

> levels. Furthermore, agency structures and cultures do not effectively address complex, polarized policy environments made up of numerous competing constituents.

Lands adjacent to the mountain national parks in the Central Rockies under the Alberta government's jurisdiction have been managed traditionally to provide high densities of ungulates and low densities of wolves (E. Bruns, Regional Biologist Alberta Environment, pers. comm.). In contrast, Banff National Park managers have recently placed emphasis on a high wolf density, low elk density system in portions of the park (C. White, Conservation Biologist Banff National Park, pers. comm.). Ironically, neither of these two management directives may result in the persistence of the wolf population. Thompson et al. (2000:1260) urged for "more integrated management bodies that include strong links between decisionmakers, scientists, and those involved at all levels of the industries concerned."

PVAs have the potential to provide the 'sideboards' necessary for conservation of large carnivores such as wolves. The population modeling process allows for the development and testing of competing hypotheses about the dynamics of the system that will help improve our understanding of the risks faced by a population and focus management priorities (Boyce 2001). Perhaps the best utility of a PVA, however, is its application in an adaptive management framework (Boyce 1992). Although the suggestion of integrating PVAs into an adaptive management strategy is appropriate for conservation, actual applications of PVA in an adaptive management context are rare (Boyce 2001). Walter's (1997) review of the failure of adaptive management in large-scale ecosystems suggests that the failure is due primarily to socio-political factors. The wolf population of the Central Rockies provides a challenge to managers and scientists to overcome the social obstacles inherent in adaptive management and the conservation of a species that has the potential, or is perceived, to compete with human interests. Undoubtedly, an inter-jurisdictional administrative group will be necessary to oversee the conservation of the wolf population. The current scenario of disjunct management direction among the various jurisdictions overseeing this population, however, runs counter to wolf conservation. We evidently need a new paradigm that promotes a coordinated inter-jurisdictional approach to the conservation of wolves that addresses the need for regional wolf persistence and well-functioning predator-prey relations and recognizes the risk of ignoring uncertainty of future anthropogenic effects on ecosystem processes.

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