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Frontispiece

“In the mountains a biologist can become an explorer in the physical realm as well as the intellectual one. Mountains are symbols of the unknown, of the mysterious force that beckons us to discover what lies beyond, that tests our will and strength against the sublime indifferences of the natural world. Research among the ranges affords the purest pleasure I know, one which goes beyond the collecting of facts to one that becomes a quest to appraise our values and look for our place in eternity. When at dusk the radiant peaks are deprived of the suns fire, leaving the gloomy and desolate cold prowling their slopes, and when later, white in the moon, the glaciers glow like veils of frozen light, all difficulties vanish in the presence of such primordial beauty”

-- George B. Schaller, Stones of Silence, 1980

University of Alberta

LINKING PREDATION RISK AND FORAGE TO UNGULATE POPULATION DYNAMICS.

by

Mark Hebblewhite

A thesis submitted to the Faculty of Graduate and Research Studies in partial fulfillment of the requirements for the Degree of *Doctor of Philosophy*

In

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Spring, 2006

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Linking Predation Risk and Forage to Ungulate Population Dynamics submitted by **Mark Hebblewhite** in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

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Dedication

To the wolves, elk, and all sentient beings of the Ya Ha Tinda.

ABSTRACT

Many ungulate populations are partially migratory, where some individuals migrate and some do not. The success of either migratory strategy is the result of differential forage selection and predation risk-avoidance. In this dissertation, I examine how multi-scale resource selection by migrant and resident elk (*Cervus elaphus*) differentially influence demography. I studied the partially migratory Ya Ha Tinda elk population, which winters in the province of Alberta and migrates in summer to Banff National Park. I reviewed population trends from 1970–2005, and found the migrant proportion declined from 95% to 60%. To examine the role of differential forage selection, I built a spatially and temporally-explicit forage model using field and remote sensing data to predict available forage biomass and quality to elk. By selecting intermediate forage biomass in phenologically delayed areas, migrants had 5% higher forage digestibility than residents. Next, I developed a spatially and temporally explicit predation risk model for wolves (*Canis lupus*), elk's main predator. Predation risk at the summer range scale was 70% lower for migrants compared to residents. Yet, despite riskier summer ranges, resident elk adopted fine-scale foraging and anti-predator strategies within these ranges to reduce the risk they experienced to only 15% higher than that of migrants. Furthermore, predation risk experienced by migrants during migratory periods was 52% higher than residents. Differences in resource selection translated to demographic differences between strategies in Leslie-matrix models. Bottom-up effects manifested in higher pregnancy rates and female calf weights for migrants. Yet top-down effects of predation by wolves and grizzly bears (*Ursus arctos*) were greater for migrants, who experienced lower adult and calf survival. Resident adult and calf survival was higher despite poorer forage because of fine-scale risk-avoidance combined with a behavioural response to live in larger group sizes in summer. The ratio of migrant to resident population growth rates from Leslie-matrix models matched the observed rate of migratory decline from 1970-2005. I conclude that given current conditions, notwithstanding potential density-dependent processes, the proportion of migrants in this population will continue to decline as a result of top-down limitation despite the significant benefits of higher forage quality from migration.

ACKNOWLEDGEMENTS

Funding for this study was provided by ACA- Challenge Grants in Biodiversity, Alberta Conservation Association, Alberta Cooperative Conservation Research Unit, Alberta Enhanced Career Development, Alberta Sustainable Resource Development, Canadian Foundation for Innovation, Centre for Mathematical Biology, Canon National Parks Science Scholarship for the Americas, Foothills Model Forest, Foundation for North American Wild Sheep, Marmot, Mountain Equipment Co-op Environment fund, National Science and Engineering Research Council (NSERC), Parks Canada, Patagonia, Red Deer River Naturalists, Rocky Mountain Elk Foundation, Sundre Forest Products Limited, University of Alberta, University of Calgary, Weyerhauser Company-Alberta Forestlands Division, and the Y2Y Science grants program. For skillfully administering this funding I thank Natalia Riley and especially Doris Simader, as well as the excellent administrative staff of the Department of Biological Sciences. This research was conducted according to UA-Animal Care protocol # 353112, Parks Canada EIA permit #BNP–00047531, and Alberta research and collection permit #'s GP4618 and CN087.

I extend the sincerest thanks to Ya Ha Tinda ranch staff for their assistance, especially ranch managers Rick Smith and John Nylund, as well as Jean Smith and Marie Nylund; Rob, Sue, Shelby, and Jordan Jennings; and Dick Levie and Helene Galt. This project would not have been possible, nor as rewarding, without their friendship and support. I especially thank their patience as I learned mountain horsemanship.

Strong logistical and administrative support from Parks Canada led this project from the beginning. Cliff White provided crucial support, vision, and liaison skills, and served as a valuable academic committee member, as well as a good friend. I also thank

Chief Park warden Ian Syme for his support and leadership that will be critical for the implications of this research to translate into management. The support of the Banff National Park (BNP) backcountry wardens, in particular Dave Norcross, facilitated remote backcountry research. I additionally thank backcountry wardens Helene Galt, Scott Ward, Barb Johnson, Chris Worobets, Steve Anderson, Anders Hawkins, and Ivan Phillips. Dave Dalman deserves special recognition for his steadfast support at a crucial early juncture. Parks Canada wildlife veterinarian Dr. Todd Shury (DVM) provided expert assistance and advice with wolf and elk capture throughout the study. Thanks also to Park wardens Tom Hurd, Ian Pengelly, Darrel Zell, Tom Davidson, Glen Peers, and the BNP dispatchers for strong support during the project duration.

I similarly benefited from strong support from the Fish and Wildlife Division of Alberta Sustainable Resource Development. I thank James Allen and Eldon Bruns for their constant assistance with aerial surveys, elk trapping, harvest statistics, as well as for wealth of advice about the Ya Ha Tinda and on negotiating new political landscapes outside of BNP. I also thank Gerald Sambrooke of Alberta Forestry for coordinating use of AB-SRD's backcountry patrol cabins, and patrolmen Frank Coggins for his cooperation. The staff at the Sundre Fish and Wildlife office, Lori Berg, Rick Smee, and Conservation Officer Jim Mitchell provided great local support and assistance.

I am indebted to the hunters, outfitters, trappers and recreationists, all expert naturalists and observers, who called the Ya Ha Tinda region home long before I began my research. Their keen insights, patience, assistance, and friendship improved this research, and it is my hope that this research provides the foundation for interagency management of this critical elk population. I thank Sam Snidemiller, Ken Fraser, Gary

Bracken, Bill McLoughlin, Roger Dye, Lorne Hindbo, Eadie Nagy, Tim Barton, Clarence Stewart and the members of the Friends of the Eastern Slopes, especially.

I sincerely thank Mike Dupuis for safe, professional, and enjoyable mountain telemetry flying. The hundreds of hours I spent with Mike in the air was one of the most enjoyable parts of the research. I will miss it. I also thank helicopter pilots from Alpine helicopters and Rocky Mountain House for providing safe aerial survey services. For wildlife capture services, I cannot thank Clay Wilson and Tony Vandenbrink of Bighorn Helicopters from Cranbrook B.C. enough. They are simply the best at what they do, and were always able to get the job done safely, humanely, and efficiently.

To successfully conduct such a large-scale study was a result of the dedicated field assistants who hiked and skied thousands of kilometers collecting data. I thank the following field assistants for their dedication, hard work, and enthusiasm: Geoff Williams, Shari Clare, Joe Litke, Robin Whittington, Bridget McClarty, Jennifer Wasylyk, Mark Lindberg, Shannon Stotyn, Helene Galt, Terry Larsen, Julia Burger, Freek Cluitmans, Janna Breitman, Monica Boguslawski, Scott Stewart, Saakje Hazenberg, Judith Wheeler, and Alison Buckingham. I especially thank Linda Thurston, Robin Munro, Cedar Muller and Holger Spaedke whose work went beyond that of technician to full collaborator. I thank Lindsay Sachro for allowing us to use her 2001 vegetation data. And I appreciate the collaboration of Greg McDermid, Department of Geography, University of Calgary, for obtaining and processing MODIS NDVI images, and assisting in their analyses in Chapter 3.

I have been fortunate to benefit from many excellent teachers during my academic career, and I thank Paul Paquet and Dan Pletscher for continuing to lend advice. I thank committee members Stan Boutin, Cormack Gates, Mark Lewis, Colleen Cassady-St.Clair, Luigi Morgantini, and Cliff White, as well as my external examiner, François Messier, for taking the time to review this dissertation, and for providing sage advice throughout its development. Greatest thanks are reserved, however, for my present advisor, Evelyn Merrill, for her belief and support in me, her insights, for challenging me when needed, and for being a friend. I must also thank a special teacher in Edmonton who has enriched my life greatly, Kushok Lobsang Damochöe of Gaden Samten Ling.

I thank my colleagues at the University of Alberta for enjoyable discussions, digressions and friendship: Merrill-lab mate #1 Jacqui Frair as well as Hawthorne Beyer, Doris Simader, Darcy Visscher, Daniel Fortin, Leslie McInenly, Nathan Webb, and others. I thank Doris Simader for copy editing the final dissertation, and Jacqui Frair for reviewing individual chapters. I also appreciated the friendship of Cam Aldridge, Joanne Saher, Cam Gillies, Scott Nielsen, Lana Ciarnello, Shannon Stotyn, Amy Hurford, Bob Lessard, Chris Jerde, and Layla Neufeld, and others. Friends further a field enriched my life including Richard Kilpert, Marco and Mimosa Musiani, Danah Duke, Melanie Percy, Cedar Mueller, Rod DeLeeuw, Mark Lindberg, Darryl Deboer, Brandon Furyk, and Pete Biro. I also thank my faithful dog Keta, and the equally faithful horses I learned much about grass and herding from, especially Cody and Banjo. I thank Bridget McClarty, without whose support I could not have succeeded to the degree I have.

Finally, I thank my family for their unwavering support, especially my mum Eileen Bennett. My brothers Nigel and Craig, and my father Keith, and cousin Jules were there whenever I needed to be reminded who I was. I thank my entire family for believing in me.

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CHAPTER ONE: DISSERTATION INTRODUCTION

AN OVERVIEW AND RATIONALE FOR LINKING UNGULATE POPULATION DYNAMICS TO RISK AND FORAGE

Ecology is the study of the interactions that determine the distribution and abundance of organisms (Krebs 1994). Two of the most important interactions must surely be predation and herbivory, recognized since Darwin's theory of natural selection (Darwin 1859). Early mathematical models linking predators to prey (Lotka 1925, Volterra 1926) were expanded to include a broader definition of consumers and resources to include primary producers (plants) and their herbivore consumers (Noy-Meir 1963, Rosenzweig and MacArthur 1963). Applied to systems of predators, herbivores, and plants, novel insights revealed the paradox of enrichment, stability, and chaos (Rosenzweig and MacArthur 1963, Caughley and Lawton 1981).

The generality of these early models necessitated a lack of detail, making specific applications difficult. As a result, ecologists began focusing on individual links of three trophic level systems. For example, Holling (1959) revealed the mechanisms of the predator-prey functional response, namely the interplay of search and handling times. Hollings' (1959) work expanded to include numeric responses, the influence of space, social behaviour, and different functional forms (Taylor 1984, Messier 1994). Predator-prey dynamics has since followed a phenomenological/statistical approach of fitting different predator-prey models to data using statistical models (Holling 1959, Messier 1994). Units are the number of prey killed per unit time and expressed as rates or proportions of the prey population (Messier 1994). In isolation of plant effects on prey, predator-prey research suggests predation may have strong “top-down” limiting/ regulatory effects on prey (Messier 1994, Post et al. 1999, Hebblewhite et al. 2002).

Concurrently, herbivore-plant dynamics, exemplified by ruminant-plant foraging ecology, focused on much smaller spatio-temporal scales because of difficulties in measuring plant availability to large herbivores. As a result, ruminant foraging ecology focused on mechanisms limiting intake using complex instantaneous functional responses (Spalinger and Hobbs 1992). Complexity arises because intake rate is influenced by plant structure, phenology, spatial arrangement, herbivore morphology and allometry, and plant defense compounds, often in non-linear and compensatory ways (Robbins et al. 1987, Spalinger and Hobbs 1992, Gross et al. 1995). Units are often expressed as instantaneous intake rates in grams or joules per unit time (Gross et al. 1995). Instantaneous functional responses can often be linked to daily intake rates using only gross approximations or simple rules (Turner et al. 1994). Annual intakes have been most frequently used to assess nutritional carrying capacity (Hobbs and Hanley 1990). In the absence of predation, such nutritional approaches indicate primary production limits herbivore populations (Frank 2005).

Unfortunately, predator-prey and plant-herbivore research have progressed largely in isolation, ignoring impacts of predation risk on herbivore functional responses or primary productivity on predation until recently (e.g., Jedrzerjeski and Jedrzerjewska 1996, Crête 1999). Optimal foraging theory (Stephens and Krebs 1986) provides a framework to include predation risk in foraging ecology. However, progress has been hampered by currency definition and differing spatial and temporal scales. Recent approaches used multi-objective programming to solve trade-offs between foraging and predation risk in simple experimental systems on short time scales (Rothley et al. 1997). While these experimental approaches provide guidance in simple systems, it is not clear how trade-offs optimized over larger spatio-temporal scales to maximize lifetime fitness. The study of predation risk is rife with theoretical approaches (Houston et al. 1993), yet few empirical examples (Gilliam and Fraser 1987) of how to convert predation risk to energetic units are used in foraging models. These few experimental approaches offer insight, and could potentially provide some answers about how to merge predator-prey and herbivore-plant dynamics.

However, recent reviews of the study of predation risk studies (Lima and Zollner 1996, Lima 2002) paint a grim picture of challenges facing such reunification. Experimental approaches often use presence or absence of predation risk when predation risk varies continuously in space and time in nature (Lima and Zollner 1996, Kristan and Boarman 2003). Experiments often use small spatio-temporal scales, increasing risk effect sizes. Even large experiments pose problems in interpretation (Turchin 2003). Furthermore, treating predators as static ignores their dynamic nature, captured only by game theoretical models where predators and prey move in response to each other (Hugie and Dill 1994, Mitchell and Lima 2002,). Such three trophic system game theory models are in their infancy, and preliminary results are critically dependent on movement rules, encounter rates, and spatial-temporal scales (Hugie and Dill 1994, Mitchell and Lima 2002). The quantitative study of animal movement provides an approach to explicitly model movements (Turchin 1998). Even adding a modest amount of realism to such behavioural movement models (e.g., directional bias for high predation risk, habitat, or human landscape features) quickly turns what could be a mechanistic approach into a statistical one, especially if such movement rules are estimated for both predators and prey. While such approaches look promising to reveal important mechanisms (i.e., encounter rates), I believe it remains doubtful whether these mechanistic models would be applicable to entire large-scale systems because of cascading complexity and the number of required parameters. Considering that many conservation problems occur at these large-scale systems (Lehmkuhl et al. 2001), methods to link predators, plants, and herbivores, even if statistically based (e.g., Franklin et al 2000), would be of great conservation value.

OBJECTIVES

The primary objective of this dissertation is to develop a statistically based approach to link ungulate populations to spatial variation in predation risk and forage resources in real ecological landscapes, thus working towards what Lima and Zollner (1996) called a “behavioural ecology of ecological landscapes”. I will study the effects of wolf predation on the Ya Ha Tinda elk population (Morgantini and Hudson 1989) in the front ranges of the Canadian Rockies in and adjacent to Banff National Park, Alberta. This elk population is partially migratory, thus exposed to wide gradients in predation risk and forage availability. The impetus for initiating this research was that both Federal and Provincial management agencies noticed an apparent decrease in migratory behaviour in this population, with a concomitant increase in the proportion of the population that was resident. These changes generated considerable management interest and concern for meeting both National park and provincial management objectives.

First, I review evidence for effects of forage and predation on the dynamics of the partially migratory elk herd using long-term changes in population numbers and distribution to test the hypothesis that migratory behaviour has declined in this population (Chapter Two). I examine mechanisms of ungulate selection for spatial and temporal variation in forage (Chapter Three) and estimate mechanisms of elk (*Cervus elaphus*) selection for wolf (*Canis lupus*) predation risk by developing spatial predation risk models (Chapter Four). These alone offer insights into mechanisms of predation and forage influence on elk populations. However, by evaluating elk resource selection at multiple spatial scales as a function of both predation risk and forage (Chapter 5), I determine the resource selection strategies used by both migrant and resident elk. Finally, in Chapter 6, I evaluate the population consequences of these resource selection strategies to adult female elk survival, calf survival, pregnancy rates and ultimately, population growth rates. By comparing population growth rates to long-term trends, I evaluate potential future trends for this elk herd. The statistical trade-off approach I will develop between forage and predation risk will have important applications to predator-prey and protected areas management by linking management actions to maintain ungulate population dynamics. For example, in my concluding chapter, I outline how the statistical framework I develop between predation risk and forage for elk can be used to evaluate cumulative effects of habitat and predator changes on herbivore population dynamics in the context of management changes in the Ya Ha Tinda ecosystem.

LITERATURE CITED

Caughley, G. and Lawton, J.H. 1981. Plant-herbivore systems. Pages 132-166 *in* R. M. May editor., Theoretical ecology. Blackwell, Oxford, UK.

Crête, M. 1999. The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. Ecology letters **2**:223-227.

Darwin, C. 1859. The origin of species. Murray, London.

Frank, D.A. 2005. The interactive effects of grazing ungulates and aboveground production on grassland diversity. Oecologia **143**:629-634.

Gilliam, J.F. and D.F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology **68**:1856-1862.

Hebblewhite, M., D.H. Pletscher, and P.C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology **80**:789-799.

Hobbs, N.T. and T.A. Hanley. 1990. Habitat evaluation - do use availability data reflect carrying-capacity. Journal of Wildlife Management **54**:515-522.

Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European sawfly. The Canadian Entomologist **91**:293-320.

Houston, A.I., J.M. Mcnamara, and J.M.C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society-Biological Sciences **341**:375-397.

Hugie, D.M. and L.M. Dill. 1994. Fish and game - a game-theoretic approach to habitat selection by predators and prey. Journal of Fish Biology **45**:151-169.

Jedrzerjeski, W. and B. Jedrzerjewska. 1996. Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. Acta Theriologica **41**:1-34.

Krebs, C.J. 1994. Ecology: the experimental analysis of distribution and abundance. HarperCollins College Publishers, New York, NY.

Kristan, W.B.I. and W.I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology **84**:2432-2443.

Lehmkuhl, J.F., J.G. Kie, L.C. Bender, G. Servheen, and H. Nyberg. 2001. Evaluating the effects of ecosystem management alternatives on elk, mule deer, and white-tailed deer in the interior Columbia River basin, USA. Forest Ecology & Management **153**:89-104.

Lima, S.L. 2002. Putting predators back into behavioural predator-prey interactions. Trends in Ecology and Evolution **17**:70-75.

Lima, S.L. and P.A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. Trends in Ecology and Evolution **11**:131-135.

Lotka, A.J. 1925. Elements of physical biology. Reprinted in 1956 by Dover Publications, New York.

Messier, F. 1994. Unuglate population models with predation: a case study with the North American Moose. Ecology **75**:478-488.

Mitchell, W.A. and S.L. Lima. 2002. Predator-prey shell games: large-scale movement and its implications for decision making by prey. Oikos **99**:249-259.

Morgantini, L.E. and R.J. Hudson. 1989. Nutritional significance of wapiti (*Cervus elaphus*) migrations to alpine ranges in western Alberta, Canada. Arctic and Alpine Research **21**:288-295.

Post, E., R.O. Peterson, N.C. Stenseth, and B.E. McLaren. 1999. Ecosystem consequences of wolf behavioural response to climate. Nature **401**:905-907.

Robbins, C.T., S. Mole, A.E. Hagerman, and T.A. Hanley. 1987. Role of tannins in defending plants against ruminants - reduction in dry matter digestion. Ecology **68**:1606-1615.

Rosenzweig, M.L. and R.H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist **97**:209-223.

Rothley, K.D., O.J. Schmitz, and J.L. Cohon. 1997. Foraging to balance conflicting demands: novel insights from grasshoppers under predation risk. Behavioural Ecology **8**:551-559.

Spalinger, D.E. and N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores - new models of functional-response. American Naturalist **140**:325-348.

Stephens, D.W. and J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.

Taylor, R.J. 1984. Predation. Chapman Hall, New York.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sunderland, Massachusetts, Sinauer Associates, Inc.

Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, Princeton, NJ.

Turner, M.G., Y. Wu, L.L. Wallace, W.H. Romme, and A. Brenkert. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. Ecological Applications **4**:472-496.

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature **118**:558-560.

CHAPTER TWO

IS THE MIGRATORY BEHAVIOUR OF MONTANE ELK HERDS IN PERIL? THE CASE OF ALBERTA'S YA HA TINDA ELK HERD.[1]

INTRODUCTION

Migratory ungulates, such as wildebeest (*Concochaetes taurinus*) in the Serengeti (Sinclair 2003) and wapiti (*Cervus elaphus*) in the greater Yellowstone ecosystem (Houston 1982), occupy a 'keystone' role in many ecosystems (Sinclair 2003) often defining ecosystems by their movements. Because of their important ecosystem role, concern for worldwide declines in migratory ungulates is mounting (Schaller 1988, Berger 2004) and causes for declines are complex and variable. In Africa, encroaching cultivation and poaching threaten the Serengeti wildebeest migration (Thirgood et al. 2004), while in Asia, market hunting has been largely responsible for migratory declines (Schaller 1988). In North America, migratory declines of elk herds have been related to differential hunting pressure on migratory segments of elk herds (Boyce 1989, Smith and Robbins 1994), anthropogenic barriers associated with oil and gas exploration along migration routes (Berger 2004), and creation of new food sources such as hay stacks that

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[1] This chapter will be submitted to Wildlife Society Bulletin for publication under the authorship of M. Hebblewhite, E. Merrill, L. Morgantini, C.White, J.R. Allen, E. Bruns, L.Thurston, and T. Hurd. Authorship reflects that data collected in this chapter is the synthesis of over 30-years of agency survey data collected by Parks Canada and AB-SRD, as well as the PhD Dissertation of L. Morgantini, Department of Renewable Resources, University of Alberta. I use the first person throughout for consistency with the rest of this Dissertation, but acknowledge other authors contributions throughout as appropriate.

when combined with hunting sanctuaries, attract elk year-round (Burcham et al. 1999). In western Canada, a 10-year decline in the ratio of migrant to resident elk in the Bow Valley elk herd of Banff National Park (BNP) was correlated with human activity that created a predation refuge from recolonizing wolves (Woods 1991, McKenzie 2001, Hebblewhite et al. 2005). Across much of western North America, ungulate populations are faced with similar complex land-use changes that threaten the long-term viability of migratory populations (Smith and Robbins 1994, Berger 2004).

I examined population and migratory dynamics of the Ya Ha Tinda (YHT) elk population in Banff National Park (BNP) to understand migratory changes and illustrated the difficulties of managing migratory populations in transboundary systems. I focused on the YHT elk herd because it is the largest elk herd in BNP and one of the largest migratory herds in Canada (Gunson 1997). The herd winters outside of BNP on the low-elevation grasslands of the YHT winter range, and although this area was removed from BNP in 1931 to AB provincial jurisdiction for natural resources, Parks Canada retained ownership of a 44-km^2 ranch for training and wintering 100-200 horses on the winter range. Controversy over horse vs. elk overgrazing (McGillis 1977, AGRA Earth and Environmental Ltd. 2000) has characterized the YHT ranch since its creation, and is a product of differing federal and provincial agency management objectives (Morgantini 1995, Clark et al. 2000). In the 1970's, almost the entire YHT population migrated 25-50 km west to summer inside BNP (Morgantini and Hudson 1988). Since the late 1990's concern has been mounting that the decline in migratory behaviour of the YHT elk herd mirrors that observed in the Bow Valley, a decade earlier.

I tested for evidence of migratory changes and evaluated hypotheses underlying migratory patterns in the YHT population. I synthesized data collected over the 1972-2005 period to test for migratory changes from three major data sources: one early telemetry study from 1977-1980 (Morgantini and Hudson 1988), federal and provincial aerial surveys and visual neck banding data from 1970-2004, and one late telemetry study during 2002-2004 (this study). Further, I identified eight hypotheses as potential causes for migratory declines, which fall into three broad categories: elk population management, habitat management, and wolf predation-related actions (Table 2-1). Because migratory elk historically remained in BNP until after the regular fall elk harvest outside BNP ended (Morgantini 1988), I predicted that fall harvests would reduce residents more than migrants, thus increasing the M:R ratio (Table 2-1: Hypothesis 1-H1). In addition, given high enough harvests, elk population size (N_t,) and population growth rate (r_t) would be reduced. Second, over 1,000 elk were relocated from YHT in the 1990s. If no bias occurred during capture, I expected no change in M:R after relocation. Thus, changes in M:R following relocation suggest relocation influenced migration (Table 2-1: H2).

Loss of migratory behaviour may also be related to habitat management. Because prescribed fires occurred over the past two decades on the summer range of migratory elk in BNP (White et al. 2003), positive effects of fire on elk (Boyce and Merrill 1991, Taper and Gogan 2002) would favor migrants and increase M:R (Table 2-1: H3). In contrast, I expected winter range habitat enhancements would benefit resident elk more than migratory elk, thus decreasing the M:R ratio (Table 2-1: H4). In either case, habitat enhancements would also be expected to increase N_t and r_t. If competition between elk and horses were limiting access to forage, a reduction in the number of horses would be expected to increase elk N_t and r_t. Residents may be expected to benefit more because residents remain on the winter range year-round and would benefit most from carry-over effects of reduced winter horse grazing on summer forage availability (Table 2-1: H5, McInenly 2003). Open access to hay fed to horses during late winter (Fig. 2-6) may be associated with elk habituation to humans, also reducing M:R over time (e.g., Burcham et al. 1999), but with uncertain effects on elk population dynamics (Table 2-1: H6).

During the late 1970's, wolves were just recolonizing the study area and considered to be established by the early 1980's (Morgantini 1988). Migration is broadly hypothesized to reduce predation risk for migrant ungulates (Bergerud et al. 1984, Fryxell et al. 1988). If true, migration would be expected to increase the M:R ratio (Table 2-1: H7). However, as an extension to this hypothesis, wolf protection in BNP led to higher wolf survival between 1987 and 2000 than adjacent provincial areas where wolves were harvested (Callaghan 2002). If harvest was high enough, survival differences could translate to higher relative wolf densities inside BNP, which could reduce the M:R ratio (Table 2-1: H8). In an additive fashion to any direct gradient, high human activity on the YHT during summer may cause wolf avoidance (Theuerkauf et al. 2003), potentially benefiting resident demography and decreasing the M:R ratio similar to the BV elk herd (Hebblewhite et al. 2005). Regardless, as an important limiting factor, predation by recolonizing wolves should reduce overall elk N_t and r_t (Hebblewhite 2005).

I used a broad hypothetico-deductive framework to examine predictions of these eight hypotheses in comparison to observed population response and change in M:R ratio (Table 2-1). If the predicted effect of a management hypothesis was consistent with observed changes in M:R, population trend helped explain elk population growth rate. I considered this strong evidence whereby that hypothesis influenced migratory and population dynamics. If a management hypothesis was related to M:R but not N_t or r_t, I considered this weaker evidence of an overall migratory effect. Finally, if a management hypothesis was consistent with elk r_t and/or N_t, but not M:R, I concluded that the management hypothesis affected migrants and residents equally.

STUDY AREA

The study area included the front and main ranges of the Canadian Rocky Mountains in BNP (51'30'' / 115'30'') and adjacent provincial lands, and was defined by movements of the YHT elk herd over a 6,000-km^2 area (Fig.1). Elevations range from 1600 m in valley bottoms to 3500 m. The study area was along the eastern slopes of the Rocky Mountains and has long, cold winters, and short growing seasons during June – August. Vegetation was classified into three ecoregions: montane, subalpine, and alpine. The montane ecoregion offers prime elk winter habitat and is dominated by lodgepole pine (*Pinus contorta*) interspersed with Engelmann spruce (*Picea engelmanii*) – willow (*Salix* spp.) areas, aspen (*Populus tremuloides*) – parkland, and grasslands. Sub-alpine and alpine ecoregions were comprised of Engelmann spruce-subalpine fir (*Abies lasiocarpa*) – lodgepole forest interspersed with willow-shrub riparian communities, subalpine grasslands, and avalanche terrain grading to open shrub-forb meadows in the alpine ecoregion. Holland and Coen (1983) provided a detailed description of the study area vegetation. Ya Ha Tinda means 'mountain prairie' in the Stoney-Sioux language, aptly describing the azonal, high elevation, 20-km^2 montane rough fescue (*Festuca* *campestris*) grasslands along the north side of the Red Deer River (Fig.1, 7). The YHT represents one of the most pristine and largest rough fescue montane grasslands left in Alberta (Willoughby 2001). The area is mixed with aspen forests, open conifer stands, willow – bog birch (*Betula glandulosa*) shrublands, and is surrounded by pine grading to spruce forests at higher elevations. Grassland soils consist of azonal prairie types, including rich orthic-black and eluviated black chernozem (McGillis 1977, AGRA Earth and Environmental Ltd. 1998).

Elk were the most abundant ungulate in the study area during the past three decades ranging from 1,500-2,500 animals (Holroyd and Van Tighem 1983), and comprised 70% of wolf diet (Hebblewhite et al. 2004). During the study, the YHT elk herd was partially migratory, with polymorphism for migrant and resident behaviour. Migrant elk usually departed the winter range in May or June for summer ranges and returned to winter ranges from late September to December (Morgantini 1988). Despite this movement into BNP in summer, elk from the YHT herd showed little interchange with other park elk herds (Morgantini and Hudson 1988, Woods 1991). The YHT elk herd winters outside BNP in the province of Alberta in one primary and two secondary winter ranges (Fig. 2-1). The primary winter range for ~90% of the elk herd (Hebblewhite 2006) is the YHT (Wildlife Management Unit, WMU 418, Fig. 2-1). The two secondary ranges include the Panther–Dormer river corners (WMU 416) and Harrison – Lost Guide creek flats (WMU 420).

Although elk dominated, white-tailed deer (*Odocoileus virginanus*), moose (*Alces alces*), mule deer (*O. hemionas*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and a remnant herd of 5-8 mountain caribou (*Rangifer* *tarandus*) also inhabit the areas. Alternate prey species population trends were not well know, but bighorn sheep have been relatively stable while deer spp., moose, goat and caribou numbers apparently declined since the mid 1980's (T. Hurd, Parks Canada, unpublished data). Hebblewhite et al. (2004) provided more information on wolf predation in this multi-prey system. Other carnivores included grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Puma concolor*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*).

METHODS

Elk Capture

Elk were captured during two separate studies ~ 20-years apart using 1 corral trap during the 1971-1980 study (Morgantini 1988), and 2 corral traps during the 2002-2004 study. In the early study (Morgantini 1988), visual neck collars were deployed on 11 adult females in 1971–1973 and 11 radiocollars (TELONICS Inc.) in 1977–1980 (7 adult female, 1 male and 2 female yearlings, 1 male calf), such that during 1977–1980, there were 22 marked elk in the population. In 2002–2004, 59 elk (70 adult female, 9 female yearlings) were marked with VHF radiocollars (LOTEK Inc.) and 20 elk (18 adult females, 2 female yearlings) with GPS 2200 or 3300 collars (LOTEK Inc). All elk were captured on the main YHT winter range between January-March of each year when migrant and residents mix in large groups. Capture locations between studies were similar: one corral trap in both studies was located <1 km apart and during 2002-2004 a second trap 3km east of the first trap to minimize potential capture bias. During both periods, radiocollared elk were relocated bi-weekly either from the ground or aerially from fixed or rotary wing aircraft. During the early 1977-1980 period, 9 neck banded elk were resighted an average of 3.3 times/summer but 2 were never sighted again, suggesting potential sightability bias (see Morgantini 1988). Because of vastly different sampling intensities (GPS collars vs. neckbands), I used collared animals to assess M:R ratio and simple watershed distribution patterns between studies.

Changes in Migration

I evaluated the M:R ratio, seasonal (spring and fall) migration dates, and the distribution of radio collared elk. I calculated population-level M:R ratio using the maximum number of elk observed from air and/or ground during summer on the YHT winter range as a proportion of the following winter's aerial count. I compared population-level M:R between early (1977–87) and late (1988–2004) periods using an unbalanced t-test. As a second measure, I compared M:R ratio of both radiocollared and neck banded elk between the early and late intensive study periods of 1977-80 and 2002-2004. Despite winter herd mixing and capture precautions, I tested for bias by comparing the M:R ratio of captured elk to the population M:R ratio during each year using chi-square tests.

I defined migration as seasonal movement between allopatric home ranges and estimated migration date as the midpoint between subsequent telemetry locations on alternate migratory ranges (Craighead 1972). I compared spring and fall migration date by calculating the probability of early and late migration dates differing under the Z-approximation to the normal distribution (Sokal and Rohlf 1995). I had no information on duration of migration for the early period. Thus, I assumed duration was similar to late period GPS-collar estimates of 5-days (M.Hebblewhite, U. of Alberta, unpublished report). I tested whether the proportion of collared elk (both radio and visual neck-bands) on summer ranges identified by Morgantini (1988) changed between early and late periods, using a chi-square test (Sokal and Rohlf 1995).

Spatial Distribution

Parks Canada and/or the AB Fish and Wildlife Division (ABFW) conducted aerial surveys in rotary-wing aircraft (Bell 206B Jet Ranger) every winter since 1972 except 1981, 1986 and 1992 (Table 2- 2), and approximately every third summer since 1977 (1977-1980, 1982-1985, 1987, 1991, 1998, 2003-2004). Surveys were conducted 1–200 m above ground level at 50–70 km/hr. Summer surveys were conducted in July during the morning (0600h–1200h) on clear sunny days when elk were on high elevation summer range and sightability was highest (Anderson et al. 1998). During summer surveys, all alpine and subalpine summer elk ranges were surveyed and key winter ranges identified by Morgantini and Hudson (1988). Telemetry data from both early and late periods confirmed that no major summer ranges were missed during surveys (Morgantini and Hudson 1988, Hebblewhite and Morgantini, U. Alberta, unpublished report). Winter aerial surveys were flown 1–2 days after heavy snowfalls in the morning (0800h–1200h) on sunny or flat light days during January or February to maximize sightability of elk (Allen 2005). Large herds (>50) were photographed for counting. Continuous participation since 1972 by an ABFW biologist (E. Bruns) during winter surveys, and by another biologist (L. Morgantini) during summer surveys for both periods (early and recent) ensured data consistency. Only winter population counts, not spatial data, were available for aerial surveys from 1972 to 1977. After 1977, herd size, general herd composition (bull, female, mixed), activity, and location was recorded and later transcribed to UTM coordinates. Locations were considered accurate only to 500m because of mapping differences over time. Agency biologists occasionally conducted surveys in another agency's jurisdiction. When surveys overlapped in the same year, I used only agency area-specific data. Because aerial survey area sometimes varied, I used the 90% kernel of aerial elk sightings to define core seasonal survey areas. For each season, I compared the spatial distribution of elk between time periods using multiple range permutation procedures (MRPP; Berry and Mielke 1983) in program BLOSSOM (Cade and Richards 2001). MRPP compares intra-group Euclidean distances to distances calculated at random (Berry and Mielke 1983) and tests the hypothesis that the spatial distribution of locations does not differ between 2 or more sampling occasions.

Factors Influencing Migration

The number of elk harvested during regular hunting seasons by resident and non-resident (outfitter) hunters from 1972 to 2004 in WMU 418 (Fig. 2-1) were obtained from registered hunter phone surveys (ABFW, unpublished reports) from 1986 to 2004 and from registered harvests prior to 1986 (Table 2-2). Hunting by First Nations is unreported and unregulated in Canada, but field estimates of First Nations harvest were obtained during years with field research and by Parks Canada ranch staff (Parks Canada, unpublished data). Late season hunts occurred after aerial surveys in January-February of 1969 –1975 and elk harvest during these hunts were recorded at game check stops and by registration (AB Fish and Wildlife, Edmonton, unpublished annual harvest reports).

Concern for overgrazing grew in the early 1990's as the YHT elk herd exceeded 2,200 elk (Fig. 2-2) and ABFW relocated elk instead of allowing controversial late season hunts to mitigate overgrazing concerns (Gunson 1997). From 1994 to 1999, 1,273 elk (Table 2-2) were relocated from YHT to locations 20-100 km away. During the first year, approximately 50% (223 elk) returned to YHT. In the second year, the return rate decreased to <10% (AB Fish and Wildlife, unpublished date) because elk were translocated further away than during the first year. Thus, I adjusted the number of elk translocated by 50% during the first year (Table 2-2).

Within BNP, Parks Canada burned an average of 4.87 km^2 per year (0–25.4 km^2, Table 2-2) per year of predominantly coniferous pine and spruce forest (81% conifer, White et al. 2003, Sachro et al. 2005) for a total of >88.0 km^2 since 1986. In the provincial portion of the study area, one prescribed burn of 7.01 km^2 was conducted in 1994 in WMU 420 and one human-caused fire burned >60.0 km^2 during fall 2001 in WMU 416. Fires only occurred in areas inhabited by migrant elk during summer. Because of delayed effects of fire on elk forage (Sachro et al. 2005), I used an index of cumulative area burned (White et al. 2005) to test effects of fires on elk (Table 2-2).

The YHT has been the subject of provincial habitat enhancement projects since 1986 (reviewed by Gunson 1997). From 1987–1990, 3.25 km^2 of shrub-encroached grasslands were mowed during July to reduce shrub (primarily bog birch) encroachment and 1.78 km^2 of the mowed area was fertilized. Shrub mowing has been the standard Ranch policy since 1982, with an average of 0.25 km^2 mowed/year on a rotational basis during June-August (Rick Smith, Parks Canada, personal communication). In 1990, 0.33 km^2 of shrub-encroached grasslands in WMU 416 were also mowed. In 1988, 3.16 km^2 of mature conifer adjacent to the winter range (Fig. 2-6) was logged and seeded with non-native grasses to enhance elk winter forage. I expected an elk response from fertilizing, mowing, and logging because of the demonstrated short-term increases in grass production (reviewed by Morgantini 1995). Similar to fire, I used an index of cumulative area of treated habitats to examine the effects of winter habitat enhancements on elk (Table 2-2).

The number of horses pastured on the YHT ranch during winter (November-May) has averaged 150 until recently when numbers have declined to <100 (Table 2-2). Horses were fed hay (*Agrostis-Dactylis-Phleum* spp. mix) during late winter (February-April). Since the late 1970's (Parks Canada, unpublished data), elk had access to hay provided for horses (Fig. 2-6). Despite scant quantitative data, hay feeding increased since the early 1990's when overgrazing concerns resurfaced, accompanied with an increased frequency of hay depredations by elk (L. Morgantini, U. of Alberta, E. Bruns, AB Fish and Wildlife, personal communication).

Wolves were extirpated throughout all of the Canadian Rockies in the 1950's by poisoning and trapping (Gunson 1992). They were considered rare during 1977–1980 (Morgantini 1988) but naturally recovered by the mid 1980's (Paquet et al. 1993). Today 30–50 wolves in 4–5 packs overlap the YHT elk population (Hebblewhite 2006). Winter wolf numbers have been surveyed in the BNP portion of the study area through radio telemetry and/or winter snowtrack surveys since the mid 1940's (Table 2-2; reviewed in Hebblewhite 2006). Unfortunately, similar wolf trend data does not exist for adjacent provincial areas. Despite the potential for effects of harvest in AB, AB population trends should be coupled with wolf numbers inside BNP because all BNP wolf packs use adjacent AB lands (Callaghan 2002). For example, the average 100% annual wolf territory size (minimum convex polygon, MCP) in the study was 1,229 km^2 (n=5, Hebblewhite 2006), indicating the large-spatial scales involved with wolf populations. Thus, I assumed wolf trends in adjacent AB areas were the same as BNP, especially in regard to recovery from extirpation during the duration of the study.

In addition to these hypothesized management variables, I included effects of summer precipitation (following Portier et al. 1999) and winter severity (Hebblewhite 2005) in population models primarily to control for climatic effects. I obtained total June through August precipitation (mm) from Environment Canada for Blue Hill tower 20 km south east of YHT for 1972–2004 (Table 2-2). I used the North Pacific Oscillation (NPO) climate index (Trenberth and Hurrell 1994) as an index of winter severity for elk (Hebblewhite 2005, available from http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

Elk Population Dynamics

Because up to 90% of the regional elk population winters in WMU 418 (YHT) (Hebblewhite 2006), I considered WMU 418 winter counts of elk as representative of the YHT elk population. I determined population growth rate (r_t) of elk wintering in WMU 418 from aerial counts and adjusted for relocation and harvest by:

$$r_t = \ln\left([N_{(t+1)} + H_{(t+1)}] \,/\, [N_{(t)} - LH_{(t)}] \right), \tag{1}$$

where r_t is the adjusted elk population growth rate, $H_{(t+1)}$ is the number of elk 'removed' (harvested) before winter surveys during year t+1, and $LH_{(t)}$ is the number of elk 'removed' (late season hunts and translocated elk) during year t after population surveys (Merrill and Boyce 1991). The numerator $[N_{(t+1)} + H_{(t+1)}]$ is the pre-hunt elk population during $N_{(t+1)}$, whereas the denominator, $[N_{(t)} - LH_{(t)}]$, is the post late hunt/relocation population size during year $N_{(t)}$. Adjusting for elk harvest and relocation approximates population dynamics in the absence of hunting (Taper and Gogan 2002). I assumed no poaching loss, crippling loss, additive harvest rates, and 100% survival between survey date and hunting/relocation dates.

I modeled how elk counts (N_t), horse numbers, wolf numbers, habitat variables, summer precipitation and the winter NPO index (Table 2-2) affected r_t over the 32-year time series. Given the *a priori* importance of density dependence, I retained elk N_t in all models and assumed linear density dependence. Despite debate regarding density dependence, linear density dependence provides a useful first step in the analysis of population dynamics (Sinclair and Caughley 1994). I examined factors at 1 time lag and included linear and non-linear climatic effects (e.g., Portier et al. 1998) by including quadratic terms. I tested the following interactions; 1) NPO and wolf numbers (Hebblewhite 2005), 2) NPO and elk density (Portier et al. 1998), and 3) summer rainfall and elk density (Clutton-Brock et al. 1982). I screened variables for collinearity >0.5, and developed a set of exploratory candidate generalized linear models (GLM's) of factors affecting elk r_t (Burnham and Anderson 1998). GLM's were of the general form:

$$r_t = \ln\left(\frac{N_{t+1}}{N_t}\right) = \beta_0 + \beta_1 elkN(t) + \beta_2 x_2(t) + ... + \beta_m x_m(t) + \varepsilon \qquad (2)$$

where t = 1 to 32 years, N is population size in year t, r_t is population growth in year t, β_0 is the intercept, $\beta_2 ... \beta_m$ are coefficients of independent variables x_2 …. x_m, and ε is Gaussian random error where $\Sigma(\varepsilon_t)=0$. GLM's were estimated using the identity link by maximum likelihood estimation in Stata 8.0 (StataCorp 2004). Models were ranked using AIC_c, and where model selection uncertainty arose, a cutoff of $\Delta AIC_c=2$ was used to estimate the top model set (Burnham and Anderson 1998). I ranked relative importance of covariates using Akaike weights following Burnham and Anderson (1998, p141). In the lexicon of Burnham and Anderson (1998), my analyses were exploratory and meant to reveal insights for further research (e.g., Chapter 3-6).

I also examined population models of elk counts unadjusted for harvest ($r_{t\text{-}raw} = ln(N_{t+1} / N_t)$) to evaluate effects of harvest on population dynamics. I estimated K by solving for N_t when r_t=0 in the harvest adjusted and raw elk models. I used Akaike weights (ω_i) to select the top model set for r_t and raw $r_{t\text{-}raw}$, and constructed unconditional parameter estimates for coefficients to estimate K (Burnham and Anderson 1998). Comparing estimates of K from r_t and raw $r_{t\text{-}raw}$ models compares the effect of harvest on elk N (Sinclair and Caughley 1994).

RESULTS

Ratio of Migrant to Resident Elk (M:R)

The average M:R observed during population surveys in the early period (12.0, SD=3.22, n=6) was higher than during the late period (3.0, SD=1.67, n=5, $t_{6,\,0.05}$=4.35, P=0.002). If the M:R had not declined, I would expect 47 residents during the late period, much lower than the average of 246 residents observed (Fig. 2-2, χ^2_1= 705.1, P<0.0001). There was slight evidence for capture bias in the M:R ratio between the captured and population estimates (χ^2_3= 7.16, P<0.03) such that the captured sample had a 6% bias towards residents. Despite this slight bias, the M:R ratio of the collared sample of elk was generally consistent with the population M:R ratio from surveys. In 1977-1980, 0 of 22 collared elk were residents. By 2003–04, 49% of 79 collared elk were year-round residents (Fig. 2-3).

Migration Dates

Migration dates were normally distributed and the average spring migration date of 9-radiocollared female elk monitored in 1978 fell within the range of spring migration dates of 79 female elk during the late period (Z-test *P*=0.53). Fall migration was 1 month earlier during the late period (Z-test *P*=0.04, Table 2-3).

Spatial Distribution

From 1977–2004, Parks Canada flew 9 surveys, ABFW flew 16 surveys, of which 3 years overlapped, and 4 years had no surveys flown by either agency resulting in a total of 22 winter surveys. I grouped winter aerial surveys into 3 periods with a balanced 7 surveys each: 1977–1986 (early), 1986–1997 (mid), and 1998–2004 (late periods) (Fig. 2-4). The 90% adaptive kernel core area for elk locations during winter surveys was 1,418 km^2 (Fig. 2-4). A shift in winter elk distribution occurred across the 3 time periods (MRPP Delta = 1.49, $P \leq 0.0001$: Fig. 2-4), with more elk observed outside BNP near YHT during the latter periods.

Between 1977 and 2004, Parks Canada and ABFW flew 12 and 1-summer surveys, respectively, resulting in 12-years of summer survey data. I grouped surveys into two relatively balanced periods with 7 and 5 surveys, respectively, 1977–1986, and 1986–2004 (Fig. 2-5) to align with winter periods. The 90% adaptive kernel core area for summer observations was 2,708 km^2 (Fig. 2-5). Summer elk distributions shifted (MRPP Delta = 1.41, P=0.0006) with noticeable declines of elk in the front ranges of BNP and increases in elk near the YHT (Fig. 2-5).

Distribution shifts observed in aerial surveys were mirrored by distributions of radio-collared elk (Fig. 2-3). Spatial distribution of collared elk differed between periods

(χ^2_1 = 20.2, P=0.003) with the largest increase in elk occurring in year-round resident elk on the YHT ranch and the greatest decline in the elk in the Lake Louise and Red Deer areas (Fig. 2-3).

Population Dynamics

The best elk population growth rate included density dependence and either a negative effect of summer rainfall and/or cumulative burn area, or a positive effect of winter-range enhancement (Table 2-4, 5). Of the three retained covariates, the effect of fire was most variable and 95% confidence intervals overlapped zero (Table 2-4). I found extreme (r>0.7) collinearity between elk N_t and cumulative hectares of winter range enhancement (r=0.80), winter wolf numbers r=(0.78), and number of horses (r=0.71). The high collinearity between elk N_t and winter range enhancement suggests caution is warranted when interpreting the top models (Table 2-4), although parameter estimates should remain relatively unbiased (Freckleton 2002). Accordingly, I considered models as exploratory. Using the sum of Akaike weights for each variable (Burnham and Anderson 1998:141), parameters were ranked in order of influence on elk population growth rate: summer rainfall ($\Sigma\omega_i$=0.545), cumulative burn area ($\Sigma\ \omega_i$=0.526), winter range habitat enhancements ($\Sigma\ \omega_i$=0.332), previous winter wolf numbers ($\Sigma\ \omega_i$=0.141), the rain*elk number interaction (ω_i=0.103), a non-linear effect of rainfall ($\Sigma\ \omega_i$=0.055), NPO ($\Sigma\ \omega_i$=0.023), NPO* elk numbers ($\Sigma\ \omega_i$=0.004), hay ($\Sigma\ \omega_i$=0.004), NPO*wolf numbers ($\Sigma\ \omega_i$=0.003), and a non-linear effect of NPO ($\Sigma\ \omega_i$=0.003). Other variables had $\Sigma\ \omega_i$=<0.0001. Based on Akaike weights, only rainfall, cumulative area burned, and habitat enhancements appeared related to elk r_t.

Solving r_t for N_t=0 using unconditional parameter estimates (β_0 and $\beta_i x_i$'s) for all top models resulted in K=1,285 (95% CI 1,098–1,471) when adjusted for hunting and management removals, and K=954 (95% CI 779—1,124, Table 2-5) without adjusting for hunting and management removals (results for $r_{t\text{-}raw}$ are not shown, Hebblewhite 2006). With hunting and management removals, the YHT elk herd was about 25% lower, or 331 fewer elk on average, than without harvest or removals.

Evaluating Predictions

Evidence from both the hypothetico-deductive framework and population dynamics models suggest observed trends in M:R ratio and population dynamics were consistent with predictions of hypotheses 4, 6, and 8, namely, winter range enhancements, habituation due to hay feeding, and a wolf protection gradient in BNP (Table 2-1, 4). However, I could not rule out potential effects of elk relocation (Table 2-1: H2). Observed elk population trends were opposite the predicted effects of elk harvest, prescribed burning, or horse numbers (Table 2-1: H1, H3 and H5). Migratory changes also were opposite of predictions if migration reduced wolf predation relative to residents (Table 2-1: H7). My population models revealed that only elk N_t, prescribed burns, summer rainfall, and perhaps habitat enhancements (Table 2-5) affected elk r_t.

DISCUSSION

My comparison of migratory and population dynamics of the YHT elk herd strongly suggests migration has changed dramatically since the 1970's. The proportion of the population migrating into BNP declined by approximately 75%, and migrant elk now return to the winter range almost one month earlier. These changes cannot be explained by changes in average abundance between the early ($\hat{N}$ =608) and late ($\hat{N}$ =917) periods because M:R declined as N_t increased. The shift in elk distribution was most pronounced from the front ranges of BNP to the YHT in winter, and a corresponding increase from <30 elk in 1977 to >300 elk summering on YHT in 2002-2004 (Fig. 2-4). While the increase in resident elk occurred during a period of general population growth, the increase at YHT in summer was greater than expected due to population growth rate alone. Therefore, despite small sample sizes of collared elk during the early period, changes in collared and population samples M:R ratio and distribution revealed the same trends of declining migration and distribution shifts to year-round residence on the winter range.

Management hypotheses whose predictions were the most consistent with migratory decline were those benefiting resident over migrant elk. These included winter range enhancement, access to hay, and possibly wolf avoidance of the YHT during summer. Resident elk would have benefited from winter range enhancements year round by summering on improved ranges without migrating. The importance of summer nutrition to elk condition and reproduction is now well documented (Cook et al. 2004). Winter range enhancements may have made winter ranges more nutritious during summer than high elevation summer ranges, given trade-offs with wolf predation risk (Hebblewhite 2006). While elk feeding on hay during winter may provide energetic benefits, a potentially important effect of hay feeding is as an attractant that leads to elk habituation to humans and loss of traditional behaviour (Burcham et al 1999, Smith 2001, Kloppers et al. 2005). Habituation to humans from hay feeding would also benefit elk in wolf avoidance of human activity on the winter range. Numerous studies have documented carnivore avoidance of high human activity (e.g., Theurkauf et al. 2003). In BNP, the town site created a predation refuge that enhanced elk survival and recruitment (Hebblewhite et al. 2005) leading to migratory declines. While human use may be lower at the YHT than in BNP, direct human-caused wolf mortality from legal hunting and trapping 10 months of the year and some illegal killing during the rest of the year (Hebblewhite 2006) may reinforce wolf avoidance of human activity (Theurkauf et al. 2003) and foster development of predation refugia, even if human use is lower than the Bow Valley.

In contrast to research elsewhere on elk and fire, I found little evidence that large prescribed fires were effective at increasing migratory elk numbers. In fact, Front Range elk herds that had access to the largest prescribed burns within BNP declined the most, and the effect of fire on population growth was weakly negative, not positive as predicted. These results may relate to how I measured effects of burning using a cumulative area burned following White et al. (2005). If effects were transitory, then a decaying effect of burns may have been observed. However, because such declines in forage biomass start to occur in stands greater than 10-20 years (Appendix 2), and many burns in the study area were <10 years old, I assumed the cumulative burn index would be useful. It was, however, difficult to completely isolate effects of burning in the study because the amount of area burned was correlated with declining elk and increasing wolf populations. Despite these caveats, however, I propose the hypothesis that in the presence of wolf predation, effects of fires are weaker, or even negative on elk (White et al. 2005). Many previous studies demonstrating positive effects of fire on elk populations occurred in the absence of wolf predation (e.g., Taper and Gogan 2002). My results at least suggest an interaction between predation by wolves and habitat restoration through fire that has important management implications for ecosystem management in National Parks (White et al. 1998). This could occur because habitat restoration through fire merely increases wolf densities because of the numeric response of wolves to elk increases to fire, and that expected ‘benefits’ to elk numbers may not be realized. Thus, management application of fire to enhance ungulates may depend on predator densities.

I suggest the hypothesized demographic benefits of migration (Bergerud et al. 1984, Fryxell et al. 1988, Table 2-1: H7) may not exist for migrants in the YHT elk herd: by all counts, residents seem to be doing relatively better. In further support, during the 1980’s, elk resided along the front-range areas of BNP during winter. However, by 2000, wintering elk populations within these areas declined or shifted to the YHT. While these trends support the existence of a predation refugium, a comparison of wolf predation on resident elk relative to forage trade-offs is required to empirically test for this effect (Hebblewhite 2006). In the absence of experimental approaches, other tools such as resource selection functions (Boyce and McDonald 1999), landscape-linked simulation models (Turner et al. 1994), or habitat linked demographic studies (Johnson et al. 2004) will be required to understand the mechanisms of how predation risk and habitat enhancement interact to influence migratory behaviour.

An important management factor not directly tested was one of the most pervasive and difficult to quantify impacts: human recreation. In the 1970’s, Morgantini and Hudson (1979) documented displacement of resident elk on the YHT by motorized use, and motorized human use was restricted in 1986. Recreational activity is now predominantly equestrian-based, which appears to disturb elk less at YHT despite overall increases in human use. Increased human activity, equestrian-based or otherwise, combined with direct human-caused wolf mortality, may repel wolves (Theurkauf et al. 2003) creating predation refugia (White et al. 1998). Further study of interactions between humans, wolves and elk on the YHT winter range is needed to confirm whether refugia leads to reduced migration, and whether a refuge is spatial (i.e., Banff townsite, Hebblewhite et al. 2005) or only temporal (e.g., Theurkauf et al. 2003). As an immediate management implication, aversive conditioning similar to what has been used on elk in the Banff Townsite (Kloppers et al. 2005) may be necessary to counteract potential predation refuge at the YHT to minimize risks of overgrazing during summer on rough fescue grasslands.

Surprisingly, the only climatic effect I found was that increased summer rainfall decreased elk r_t, similar to Clutton-Brock et al. (1982). Increased precipitation during June-August often produced snow in the Rocky Mountains, and may delay spring plant phenology that is critical for calf survival (Post and Klein 1999). I speculate the main effect of rainfall on elk r_t may be through reduced calf survival during wetter, colder summers, because of the frequency of spring/summer snowfall during wetter summers (Holland and Coen 1983). Calf survival would decrease in such summers as a result of delayed phenology reducing milk production, and increased neonatal mortality with cold temperatures. Winter severity, measured by the NPO, was also unrelated to r_t at t=0-2 lags. Nearby in the BV, severe winters interacted with high densities to reduce r_t because wolf killing rates increased with winter severity (Hebblewhite 2005). Although the NPO correlates strongly with climate on the eastern slope of the Rockies (Trenberth and Hurrell 1994), azonal climatic conditions characterizing YHT (Morgantini 1995) may have weakened the climatic signature of NPO. Alternately, because the population did not spend much time near *K*, density-climate interactions may have not occurred.

The population models also have important implications for long-term controversies surrounding range management at the YHT. I found the assumption of simple linear density dependence was warranted, similar to elk studies elsewhere (e.g., Lubow and Smith 2004, Merrill and Boyce 1991, Clutton-Brock et al. 1982), and estimated carrying capacity (*K*) based on this density dependence. In comparison to studies elsewhere without predation by wolves (Lubow and Smith 2004, Merrill and Boyce 1991), my estimates of *K* represent ecological carrying capacity given human and natural predation over 1972-2005, rather than food-based *K* or predator-regulated K (Sinclair and Caughley 1994). Long-term K under predator regulation may in fact be substantially lower than 1000 (Chapter 6, Messier 1994). Hunting and relocations reduced long-term elk numbers by an average of 22% from ~1,285 to ~985, closer to sustainable range-capacity assessments of *K* (e.g., AGRA Earth and Environmental 1998). With or without hunting or relocations, long-term equilibrium for the population is towards an *N* that was well (<55%) below the maximum observed number of elk of ~2,200. This peak in elk numbers occurred after a series of intermediate precipitation summers and immediately after fires in BNP and winter range enhancements, and may represent a short-term overshoot of *K*. In this context, elk management (hunting and relocation) was effective at reducing elk N_t closer to the 1,000 elk recommended based on range assessments for rough fescue conservation (McGillis 1977, AGRA Earth and Environmental 1998). However, at the time range assessments were done, 170-200 horses were wintered at YHT. With recent declines of horses at YHT, it may be worthwhile revisiting range assessments for grassland conservation.

Differences in resource management policies between federal and provincial agencies across jurisdictional boundaries have facilitated creation of spatial gradients in predation risk and habitat that appear to favor resident elk over migrants. National park policies protect wolves while provincial policies include liberal wolf harvests to promote elk population goals (Gunson 1997). Inside BNP, management seeks to reduce the negative effects of human recreation (Parks Canada 1997), while the province of Alberta has a more liberal recreation policy for the YHT area (Anonymous 1986). Direct wolf mortality and indirect wolf avoidance of higher human activity at YHT are therefore emergent properties of the present transboundary management policy framework. Similarly, Parks Canada seeks to restore long-term ecological conditions through application of prescribed fire to elk summer ranges (White et al. 1998), while the Alberta government had a more conservative forest-fire suppression program, albeit with increased interest in a prescribed fire program. Alberta provincial habitat enhancement policy has instead been focused on elk winter range enhancement, whereas Parks Canada's main objectives for the winter range have been horse grazing and hay feeding (Parks Canada 1987). These contrasting management objectives point to a need for development of a common interest approach to the transboundary management of the YHT elk herd (Clark et al. 2000). Historically, there was little effective coordination of management activities across the park boundary, though recent coordination efforts should be continued and strengthened (e.g., Parks Canada 2002). For example, the Bighorn cutblocks and the prescribed fire programs were implemented by provincial and federal agencies without regional assessment of their effects on the YHT elk herd. I define common interest as a set of objectives, goals or targets shared by, in this case, provincial and federal management agencies with respect to the YHT. Such common interests may include maintaining rough fescue grasslands, managing human use, preventing growth of resident elk populations, etc. I contend that transboundary management must be coordinated through development of a common interest approach such as through an interagency planning-process (Clark et al. 2000).

Transboundary management of migratory elk herds will be increasingly important because the factors that changed migration of the YHT elk herd occur elsewhere across western North America (e.g., White and Garrott 2005). My analyses indicate that isolating individual factors responsible for migratory changes with certainty will be difficult in complex management settings. I suggest there is sufficient evidence to indicate that recolonization by wolves, winter range habitat enhancement, and attraction to hay have contributed to migratory change by shifting relative benefits to elk remaining resident year-round. Therefore, these factors merit primary consideration in future management of the YHT elk herd. With recovering wolf populations present or imminent in many areas of western United States, many elk herds will face this new factor as an influence on migratory behaviour. Park and wildlife managers should be alert for migratory changes in elk populations given the important ecosystem ramifications of migration, and the implications of changes in migration for park management. For example, in BNP wolf and grizzly bear population viability ultimately depend on the density of elk as their primary prey (Carbone and Gittleman 2002) and are thus dependent on continued transboundary migrations. My research provides an illustration of the vital role areas outside-protected areas have in ecosystem management of national parks (Groom et al. 1999). National parks with transboundary populations of migratory ungulates may want to increase cooperative management with adjacent agencies to ensure key park processes are maintained.

Table 2-1. Hypotheses for effects of different classes of management actions, and their predicted effects on migratory behaviour and population size of the YHT elk herd, Alberta, 1970-2005. Management actions are predicted to increase (+) or decrease (-) the proportion of migrants and overall population size (N). Observed trends in M:R and N over the 30-year period are presented for comparison. Predictions are in bold where they match observations.

		Predicted effect on			Observed change		Consistent with	
Management Action	Hypothesis	M:R	N[a]	Mechanism	M:R	N[a]	M:R	N[a]
H1: Elk harvest	Differential harvest of resident elk should cause M:R to increase.	+	-	Elk harvest disproportionately reduces residents because most migrants do not return to the YHT for the whole hunting season.	-	+	No	No
H2: Elk relocations	Removal of 1,044 elk from YHT caused migrants to decline	-?	-[b]	Capture bias for migrant elk would reduce migrants and/or disrupt learned migratory behaviour.	-	**-[b]**	**Yes**	**Yes[b]**

H3: Prescribed fire	Burning on summer ranges should increase migrant elk.	+	+	Burning increased forage in predominantly conifer burns available to migrant elk (Sachro 2005).	-	+	No	**Yes**
H4: Winter range enhancements	Winter range enhancements increase resident elk numbers.	-	+	Resident elk remain on winter range all year, benefiting from enhanced forage during summer as a result of habitat enhancements (Morgantini 1994).	-	+	**Yes**	**Yes**
H5: Winter horse numbers	Declining horse numbers released elk from range competition (McInenely 2003).	-	+	Fewer horses should increase elk, and decrease M:R ratio because resident elk increase due to carry over effects of winter horse grazing in summer.	-	n/a[c]	**Yes**	No[c]

H6: Hay feeding	Prolonged access to artificial food source contributed to migratory decline	-	+	Hay feeding increased human habituation of residents and reduced migration (Burcham et al. 1999).	-	+	**Yes**	**Yes**
H7: Wolf predation	Spatial separation through migration reduced relative predation risk for migrants	+	-	Migrant elk should have lower predation risk (Bergerud 1984), but recolonizing wolves would still be predicted to reduce elk population size (Hebblewhite et al. 2002)	-	+	No	No

H8: Provincial wolf harvest	Differential harvest of wolves in province surrounding YHT reduced predation on resident elk	-	-	Wolf protection in BNP would reverse the relative benefits of migration under the spatial separation hypothesis, overall elk N still decline (Hebblewhite et al. 2002)	-	+	**Yes**	No

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[a] Note predicted effects of hypotheses on N_t and r_t are the same.

[b] Overall population increased (Fig. 2-1), but declined following relocations. This prediction was only compared to the post-relocation time period.

[c] Horses only started declining (Table 1- 2) following elk relocations, and during this period elk numbers were stable (Fig. 2-2) as a result of release from competition after relocation.

Table 2-2. Time-series of elk data and potential factors influencing temporal population dynamics of the YHT elk herd (WMU 418), 1970 to 2005, Alberta. Elk data include winter elk count (N_t) and maximum summer count of residents (N_{R-t}) on YHT. Population factors include the total June –August precipitation, BNP wolf abundance index, number of elk translocated, total number of elk harvested, winter horse numbers, cumulative area (ha) burned in the provincial and BNP portions of the study area, and cumulative area (ha) of winter range habitat enhancement projects.

Year[a]	WMU 418 winter elk count N_t[a]	Max. summer resident count N_{R-t}[b]	June-august precip. (mm)[c]	BNP wolf No. [d]	No. elk relocated	Total elk harvest[e]	No. of horses [f]	Cum. burn area (km^2)	Cum. winter range enhance-ments (km^2)
1973	700		277.2	9		133		0	0
1974			78.4	5		124		0	0
1975			78.8	11		33		0	0
1976	807		194.2	4		53		0	0
1977	356	34	125.3	4		56	186	0	0
1978	351	25	97.3	5		92		0	0
1979	334	25	203.4	5		135		0	0
1980	358		88	5		74		0	0
1981	278		174.3	10		170		0	0
1982	422		354.4	7		130		0	.25
1983	378		182.1	16		186		0	.5
1984		75	221.1	23		160		0	.75
1985	217	50	127.2	21		126		0	1.0
1986	200		77.9	20		76		4.17	1.25
1987	1058	75	298.5	18		124		4.17	3.04

1988	620		209.3	25		150		4.17	6.94
1989			180.4	29		170	180	6.53	7.67
1990	758		140.6	30		181	183	21.63	8.00
1991	918		245.6	35		68	196	21.63	8.25
1992	1075		179.5	24		65	171	21.63	8.50
1993	1052		262.6	30		65	189	21.63	8.75
1994	1285		257.1	35	229[g]	67	190	43.02	9.00
1995	1534		370.6	24	132	67	152	43.02	9.25
1996	1642		99.6	25	324	78	.	43.02	9.50
1997	952		163.6	35	139	67	146	43.02	9.75
1998	901		313.4	31	135	121		43.02	10.0
1999	976		129.1	25	85	87	153	45.73	10.25
2000	843	200	178.6	25		91	155	63.81	10.5
2001	931	150	187.3	26		65	144	63.81	10.75
2002	991	324	73.9	36		98	147	130.05	11.0
2003	916	253	83.2	32		107	127	130.05	11.25
2004	848	267		29		118	95	130.05	11.50
Mean	931	240.2	182.34	20.5	90.6	105.5	161.6	27.13	5.04
SD	412.0	110.20	84.043	10.98	108.03	41.77	28.74	39.799	4.634

[a] Year 2004 refers to biological year 2003/04 from June 1 2003 to May 31, 2004.

[b] Maximum number of resident elk counted on winter range WMU 418 during summer (June 1-Aug 31).

[c] Total precipitation (mm) for June, July, and August from Blue Hill Environment Canada weather station.

[d] Wolf population index derived in Hebblewhite (2006).

[e] Elk harvest includes all age-classes, and elk killed by guides, resident, non-resident, and native hunters.

[f] Number of horses wintered at YHT includes brood mares and horses being trained.

[g] Only elk that did not return to YHT following relocation (ABFW, unpubl.data)

Table 2-3. Mid points of spring and fall migration dates of radiocollared elk in the YHT population for early (1978) and late periods (2002, 2003), BNP, Alberta.

		Spring migration				Fall migration			
Period	Year	Date	SD	Range	N	Date	SD	Range	N
Early	1978	June 3	14.2	17.1	9	Nov 5	8.54	33.1	7[a]
Late	2002	June 9	14.4	12.2	20	Sept 30	25.8	13.5	16[a]
	2003	June 1	13.2	15.6	41	Oct 30	27.2	17.1	38[a]
Average Late		June 4	11.5	14.5	61	Oct 2	27.1	16.0	54

[a] Fall N is consistently lower than Spring N due to mortality, collar failure, etc.

Table 2-4. Population growth rate (***r_t***) model selection for the YHT elk population, winters 1970 to 2004. Following Burnham and Anderson (1998), R^2 is reported from general linear models, N, K, the LL, ΔAIC_c, AIC weight.

Model rank and structure	R^2	N	K	LL	ΔAIC_c	AIC weight
1- ElkN[a] + Rain[b]	0.33	25	3	7.979	0	0.163
2- ElkN + Burn[c] + HE[d]	0.35	25	4	9.244	0.325	0.139
3- ElkN + HE	0.33	25	3	7.644	0.669	0.117
4- ElkN + Burn	0.28	25	3	7.344	1.268	0.087

Notes: I only report models within 0-2 ΔAIC_c.

[a] Elk N_t is the post harvest elk N_t.

[b] Average summer rainfall (mm) measured at Blue Hill tower, 20 km SE of YHT

[c] Cumulative area burned (km^2)

[d] Cumulative area affected by winter range habitat enhancements (km^2)

Table 2-5. Model averaged parameter estimates and unconditional SE's for the top harvest/removal adjusted r_t elk population growth rate models for the YHT elk herd, 1970 to 2004.

	$r_{t\text{-}adj}$ Model	
Parameter	β	SE
Intercept	**0.440**	0.0904
Elk N_t[a]	**-0.00034**	0.000045
Rain[b]	**-0.00034**	0.000127
Burn[c]	-0.0009	0.0027
Habitat Enhancement[d]	0.0154	0.0144

Notes: Bolded parameter estimates are statistically significant at P=0.05. [a] Elk N_t is raw elk count in $r_{t\text{-}raw}$ model, and post harvest elk count in the r_t model.

[b] Average summer rainfall (mm) measured at Blue Hill tower, 20 km SE of YHT

[c] Cumulative area burned (km^2) in BNP.

[d] Cumulative area of YHT winter range enhancement (km^2).

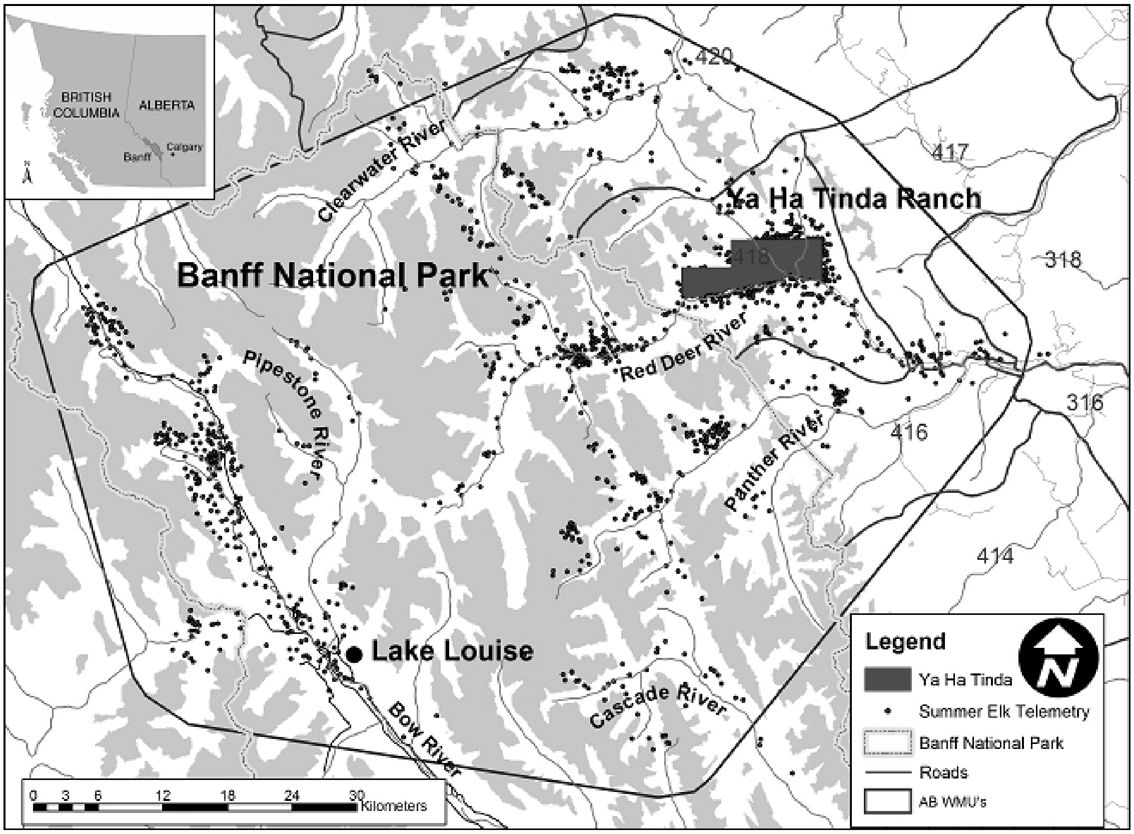


Fig. 2-1. Location of the YHT study area on the eastern slopes of BNP, Alberta, Canada, showing YHT Ranch, major rivers, Alberta WMU's, and distribution of radiocollared elk from 2001 to 2004 during summer. Areas above 2300m are shaded grey.

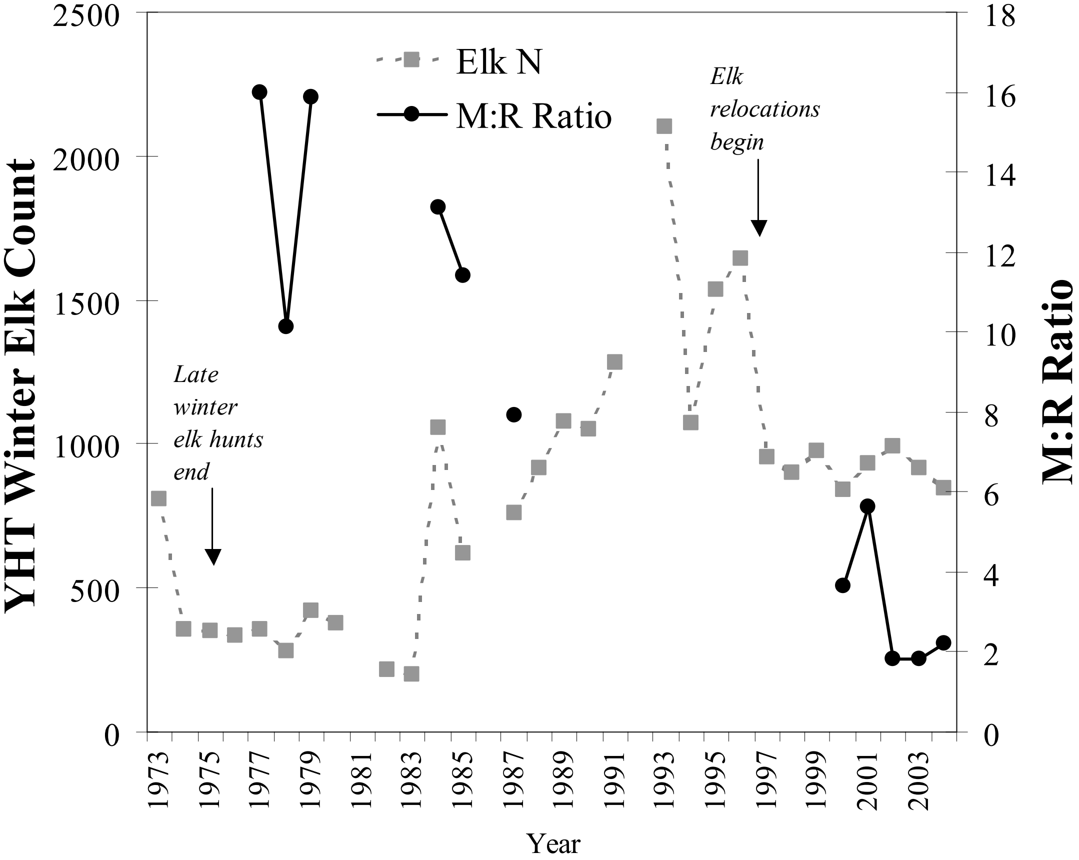


Fig. 2-2. Winter aerial survey counts of elk from 1973 to 2004 in WMU 418, AB (■), and migrant to resident ratio (M:R) of elk (■). End of the late season elk hunt and elk relocations are shown.

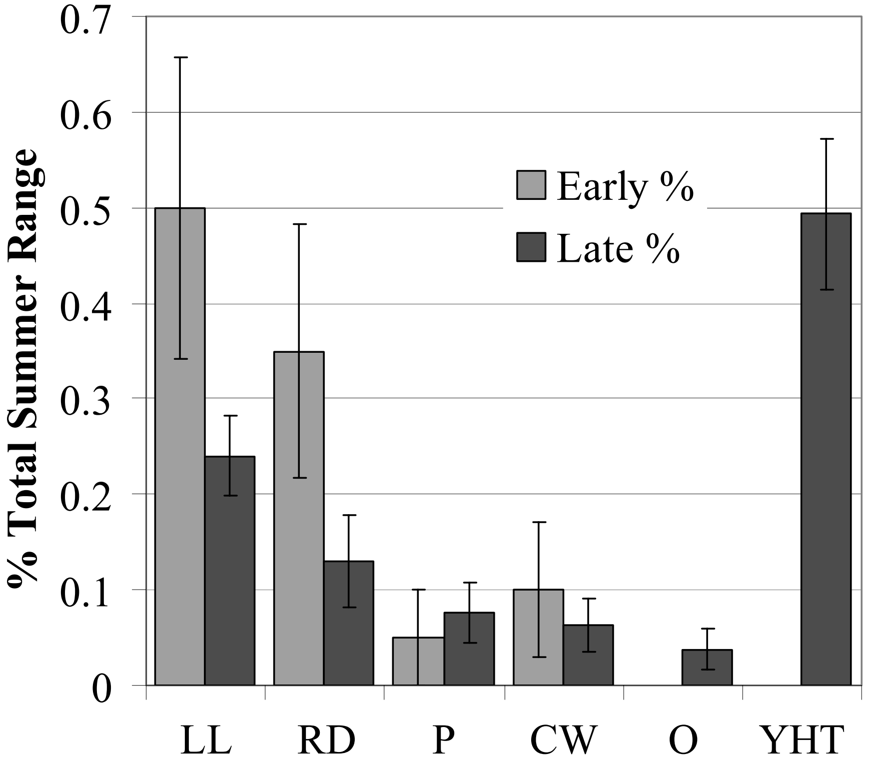


Fig. 2-3. Distribution of radiocollared elk during the early (1978, n=20) and late (2002-2003, n=79) periods within major summer range areas identified by Morgantini and Hudson (1988). LL- Lake Louise, RD- Red Deer, P-Panther, CW-Clearwater, O-Other and YHT- Ya Ha Tinda winter range. Standard errors calculated assuming binomial errors.

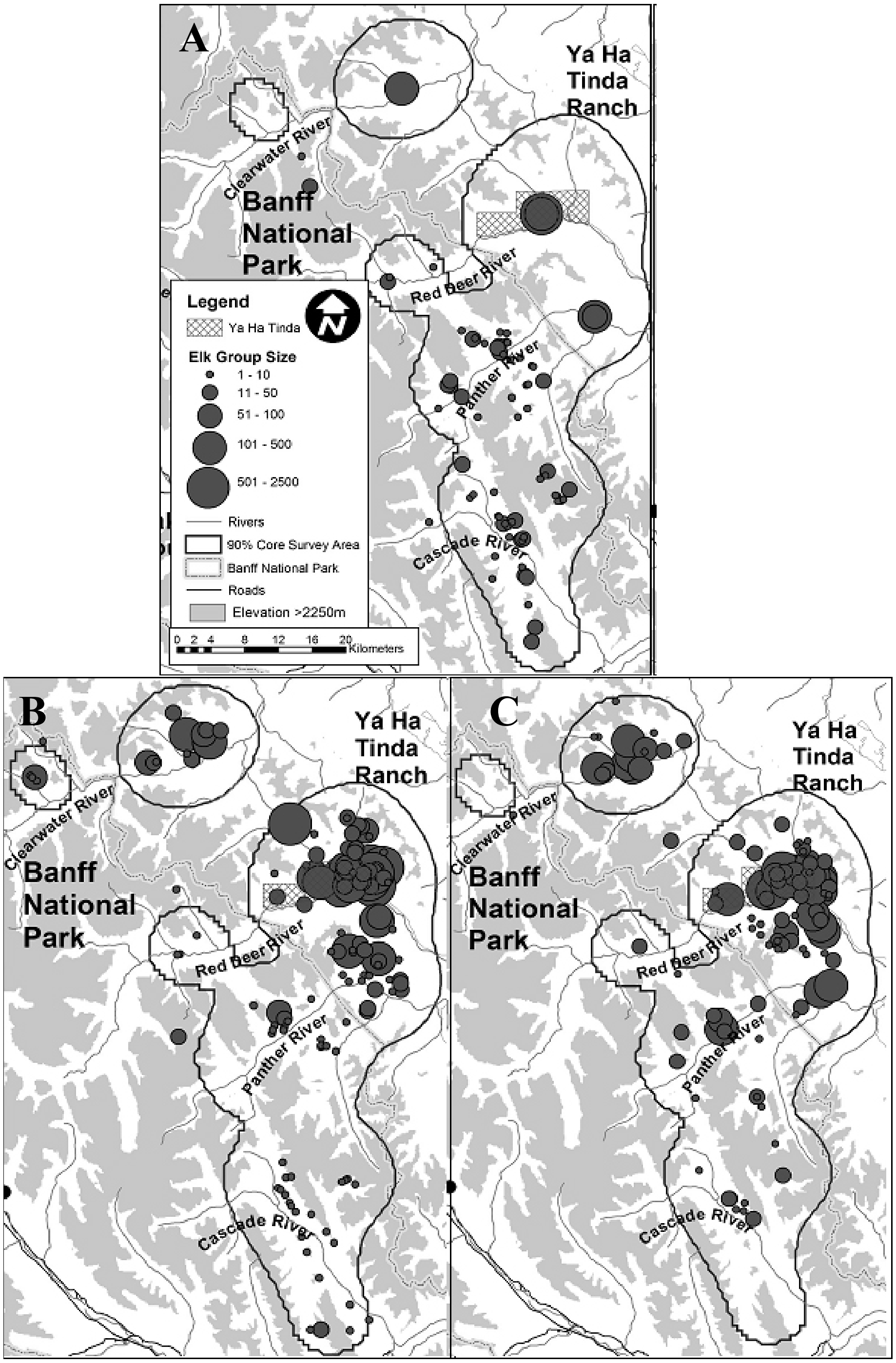


Fig. 2-4. Winter elk distribution (February/March) during a) early (1977-1985), b) mid (1986-1994) and c) late (1995-2004) study periods in the YHT elk population, BNP, Alberta, Canada. Outline shows the 90th percentile of all aerial observations.

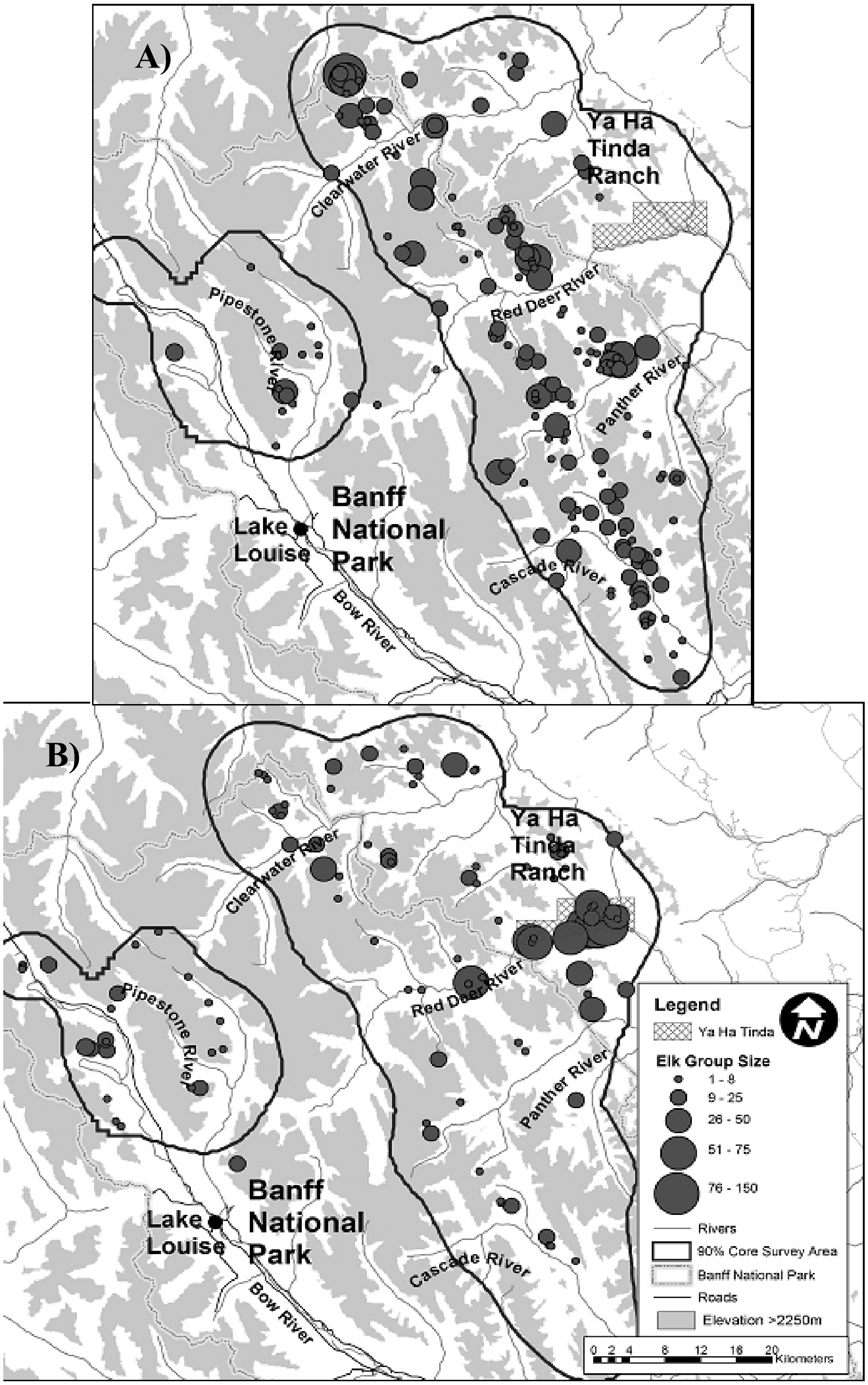


Fig. 2-5. Summer elk distribution of elk (July/Aug) during a) early (1977-1986) and b) late (1986-2004) study periods in the YHT elk population, BNP, Alberta, Canada. The area within which 90% of all aerial observations occurred is shown in the outline. Number of surveys flown per period was equal.

Fig. 2-6. Elk feeding on hay for horses during winter, YHT Ranch, 2003.

Fig. 2-7. View of YHT grasslands from the south looking north across the Red Deer River up Bighorn Creek (Cutblocks).

LITERATURE CITED

AGRA Earth and Environmental Ltd. 1998. Panther corners upper red deer range inventory. Report on file with AB Fish and Wildlife Division, Edmonton, AB. 71pp.

Allen, J. R. 2005. Use of sightability models and resource selection functions to enhance aerial population surveys of elk (*Cervus elaphus*) in Alberta. Masters of Science thesis, University of Alberta, Edmonton, AB, Canada.

Anderson, C.R., D.S. Moody, B.L. Smith, F.G. Lindzey, and R.P. Lanka. 1998. Development and evaluation of sightability models for summer elk surveys. Journal of Wildlife Management **62**:1055-1066.

Anonymous. 1986. Nordegg-Red Deer River sub-regional integrated resource plan. Alberta Forestry, Resource Evaluation and Planning Division, Edmonton, Canada.

Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology **18**:320-331.

Bergerud, A.T., H.E., Butler, and D.R., Miller. 1984. Antipredator tactics of calving caribou - dispersion in mountains. Canadian Journal of Zoology **62**:1566-1575.

Berry, K.J., and P.W. Mielke. 1983. Computation of finite population parameters and approximate probability values for multi-response permutation procedures (MRPP). Communications in Statistics-Simulation and Computation **12**:83-107.

Boyce, M.S. 1989. The Jackson Elk Herd: intensive wildlife management in North America. Cambridge University Press, Cambridge, UK.

Boyce, M. S. and E. H. Merrill. 1991. Effects of 1988 fires on ungulates in Yellowstone National Park. Proceedings of the Tall Timbers Fire Ecology Conference **17**: 121-132.

Boyce, M.S., and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution **14**:268-272.

Burcham, M., W.D. Edge, and C.L. Marcum. 1999. Elk use of private land refuges. Wildlife Society Bulletin **27**:883-839.

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Cade, B.S., and Richards. J.D. 2001. Blossom statistical software. U.S. Geological Survey, Midcontinent Ecological Science Center, Fort Collins, CO, USA.

Callaghan, C. 2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival, and persistence in the Central Rocky Mountains, Canada. Department of Zoology, University of Guelph, Guelph, ON.

Carbone, C., and J.L. Gittleman. 2002. A common rule for the scaling of carnivore density. Science **295**: 2273-2276.

Clark, T. W., D. Casey, and A. Halverson. 2000. Developing sustainable management policy for the National Elk Refuge, Wyoming. Bulletin Series, Yale School of Forestry and Environmental Studies. Yale University, New Haven, CT, USA.

Clutton-Brock, T.H., F.E. Guiness, and S.D. Albon, 1982. Red Deer: behaviour and ecology of two sexes. University of Chicago Press, Chicago, USA.

Cook, J. G., B.K. Johnson, R.C. Cook, R.A. Riggs, T. Delcurto, L.D. Bryant, and L.L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs, **155**: 1-61.

Craighead, J. J., Atwell, G. and B.W. O'Gara. 1972. Elk migration in and near Yellowstone National Park. Wildlife Monographs, **29**:1-44.

Freckleton, R. P. 2002. On the misuse of residuals in ecology: regression of residuals vs mutliple regression. Journal of Animal Ecology **71**: 542-545.

Fryxell, J.M., J. Greever, and A.R.E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist **131**: 781-798.

Groom, M., D.B. Jensen, R.L. Knight, S. Gatewood, L.S. Mills, D. Boyd-Heger, and M.E. Soulé. 1999. Buffer zones: benefits and dangers of compatible stewardship. Pages 171-198 *in* Soulé, M.E and J. Terborgh, editors. Continental Conservation: Scientific Foundations of Regional Reserve Networks The Wildlands Project, Island Press, Washington, D.C.

Gunson, J.R., 1997. Elk management plan for Alberta. Wildlife Management Division, Alberta Environmental Protection, Natural Resource Service, Edmonton, Canada.

Gunson, J.R., 1992. Historical and present management of wolves in Alberta. Wildlife Society Bulletin **20**:330-339.

Hebblewhite, M., 2005. Predation interacts with the North Pacific Oscillation (NPO) to influence western North American elk population dynamics. Journal of Animal Ecology **74**: 226-233.

Hebblewhite, M. 2006. Linking predation risk and forage to partially migratory ungulate population dynamics. Dissertation. University of Alberta, Edmonton, AB, Canada.

Hebblewhite, M., C.A. White, C. Nietvelt, J.M. McKenzie, T.E. Hurd, J.M. Fryxell, S. Bayley, and P.C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology **76**: 2135-2144.

Hebblewhite, M., P.C. Paquet, D.H. Pletscher, R.B. Lessard, and C.J. Callaghan. 2004 Development and application of a ratio-estimator to estimate wolf killing rates and variance in a multiple prey system. Wildlife Society Bulletin **31**: 933-946.

Holland, W. D. and G.M. Coen, 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 1: Summary. AB Institute of Pedology, Edmonton, AB.

Holroyd, G.L., and K.J. Van Tighem, 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 3. The wildlife inventory. Canadian Wildlife Service, Edmonton.

Houston, D. B. 1982. The Northern Yellowstone elk: Ecology and management. Macmillan Publ. Co., New York, NY, USA.

Johnson, C.J., M.S. Boyce, C.C. Schwartz, and M.A. Haroldson. 2004. Modeling survival: application of the multiplicative hazards model to Yellowstone grizzly bear. Journal of Wildlife Management **68**: 966-974.

Kloppers, E. L., St Clair, C. C. and T.E. Hurd. 2005. Predator-resembling aversive conditioning for managing habituated wildlife. Ecology and Society, **1**0: 31 [online] URL http://www.ecologyandsociety.org/vol10/iss1/art31/

Lubow, B. C. and B. L. Smith. 2004. Population dynamics of the Jackson elk herd. Journal of Wildlife Management, **68**: 810-829.

McGillis, J.R.W., 1977. Range management of the Ya Ha Tinda. Canadian Wildlife Service, Edmonton, AB, Canada.

McInenly, L.E. 2003. Seasonal effects of defoliation on montane Rough Fescue (*Festuca campestris* Rydb.). University of Alberta, Edmonton, AB, Canada.

McKenzie, J.A. 2001. The selective advantage of urban habitat use by elk in Banff National Park.University of Guelph, Guelph, ON, Canada.

Merrill, E.H., and M.S. Boyce, 1991. Summer range and elk population dynamics in Yellowstone National Park. Pages 263-273 *in* Keiter, R. B. and M.S. Boyce. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press. New Haven, MS, USA.

Morgantini, L.E. 1988. Behavioural adaptive strategies of wapiti (*Cervus elaphus*) in the Canadian Rocky Mountains.University of Alberta, Edmonton, Alberta.

Morgantini, L.E., 1995. The Ya Ha Tinda: an ecological overview. Canadian Heritage, Parks Canada, Calgary, AB, Canada.

Morgantini, L.E., and R.J. Hudson. 1979. Human disturbance and habitat selection in Elk. Pages 132-139 *in* M.S. Boyce and L.D. Hayden-Wing editor. North American Elk: ecology, behaviour, and management. University of Wyoming. Laramie, USA.

Morgantini, L.E., and R.J. Hudson.1988. Migratory patterns of the wapiti, Cervus elaphus, in Banff National Park, AB. Canadian Field Naturalist **102**:12-19.

Parks Canada. 1987. Ya Ha Tinda Management Plan. Parks Canada, Department of Canadian Heritage, Banff, AB, Canada.

Parks Canada. 1997. Banff National Park Management Plan. Parks Canada, Department of Canadian Heritage, Banff, Canada.

Parks Canada. 2002 Regional forest management strategy: Banff National Park. Environmental Screening Report. Parks Canada, Department of Canadian Heritage, Banff, AB, Canada.

Paquet, P.C. 1993. Summary reference document - ecological studies of recolonizing wolves in the central Canadian Rocky Mountains. Prepared by John/Paul & Associates for Parks Canada, Banff National Park Warden Service, Banff, AB, Canada.

Portier, C., M. Festa-Bianchet, J M. Gaillard, J.T. Jorgenson, and N.G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology, London **245**:271-278.

Post, E., and D.R. Klein. 1999. Caribou calf production and seasonal range quality during a population decline. Journal of Wildlife Management **63**:335-345.

Sachro, L. L., Strong, W. L. and C.C. Gates. 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Journal of Environmental Management, **77**: 183-193.

Schaller, G.B. 1988. Wildlife of the Tibetan Plateau. University of Chicago Press, Chicago, USA.

Sinclair, A.R.E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **358**:1729-1740.

Sinclair, A.R.E., and G. Caughley, 1994. Wildlife ecology and management. Blackwell Science, London, UK.

Smith, B. L. 2001. Winter feeding of elk in western North America. Journal of Wildlife Management, **65**: 173-190.

Smith, B. L. & Robbins, R. L. 1994. Migrations and management of the Jackson Elk Herd. U.S. Department of the Interior, National Biological Survey, Washington, D.C., USA.

Sokal, R.R., and F.J. Rohlf, 1995. Biometry. W.H. Freeman and Company, New York.

StataCorp 2004. Stata 8.0. College station, TX, USA.

Taper, M.L., and P.J. Gogan. 2002. The northern Yellowstone elk: density dependence and climatic conditions. Journal of Wildlife Management **66**:106-122.

Theuerkauf, J., Jedrzejewski, W., Schmidt, K., and Gula, R., 2003. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). Journal of Wildlife Management 67:706-716.

Thirgood, S., A. Mosser, S. Tham, G., Hopcraft, E. Mwangomo, T. Mlengeya, M. Kilewo, J. Fryxell, A.R.E. Sinclair, and M. Borner. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. Animal Conservation **7**:113-120.

Trenberth, K.E., and J.W. Hurrell.1994. Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics **9**:303-319.

Turner, M.G., Y. Wu, L.L. Wallace, W.H. Romme, and A. Brenkert.1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. Ecological Applications **4**:472-496.

White, C. A., Olmsted, C. E. and C.E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Widlife Society Bulletin **26**: 449-462.

White, C. A., Pengelly, I. R., Rogeau, M P. and D. Zell. 2003. Landscape fire regimes and vegetation restoration in Banff National Park. Parks Canada Occasional Paper BNP-2003-01. Parks Canada, Banff, Alberta, Canada.

White, C.A., T.L. Hurd, M. Hebblewhite, and I.R. Pengelly. 2005. Mitigating fire suppression, highway, and habitat fragmentation effects in the bow valley ecosystem: preliminary evaluation of a before-after-control-impact (BACI) design with path analysis. Innes, J. and Jones, G. Monitoring the effectiveness of biological conservation. Ministry of Forests, Ministry of Water, Air, Lands, Vancouver, Canada.

White, P. J. and Garrott, R. A. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. Biological Conservation, **125**: 141-152.

Willoughby, M. 2001. The rough fescue dominated community types in the foothills of north-central Alberta. Volume T/017. Public Lands Division, Sustainable Resource Development, Edmonton, Canada.

Woods, J.G. 1991. Ecology of a partially migratory elk population. University of British Columbia, Vancouver, Canada.

CHAPTER THREE

A MULTI-SCALE TEST OF THE FORAGE MATURATION HYPOTHESIS IN A PARTIALLY MIGRATORY ELK POPULATION

INTRODUCTION

Migration is thought to have evolved as a strategy to maximize fitness in the face of seasonal and spatial variation in resources (Boyce 1979, Swingland and Greenwood 1983). Large vertebrate herbivores, such as ruminant ungulates, are often migratory (Berger 2004), and while migration can also reduce predation risk (Fryxell et al. 1988), selection for forage quality is proposed as the primary mechanism driving migration in ungulates (McNaughton 1984). Migration allows animals to exploit forage quality over larger scales than non-migratory residents, and even small increases in forage quality has increased significance for ruminants because of the ‘multiplier effects’ of higher nutrients and reduced rumination on passage time (White 1983). Forage quality is highest in new growth because of high cell soluble content, which declines as plants mature and fiber accumulates (Van Soest 1982). Thus, by following spatio-temporal patterns in new plant growth, or ‘green waves’, ruminant ungulates are expected to maximize energy intake rates (e.g., Fryxell et al. 2004).

Recent studies, however, suggest energy intake is not simply a function of quality, but of trade-offs between quality and quantity (Fryxell 1991). Daily intake rates are constrained by either plant cropping or digestion (Spalinger and Hobbs 1992, Gross et al.

1993), which change in importance as biomass increases. At high biomass, when encounters with plants are not limiting, intake rates are limited by processing (e.g., chewing) constraints on intake (Spalinger and Hobbs 1992). As biomass increases, however, digestion and passage declines because of increasing fibre content (Spalinger and Hobbs 1992, Gross et al. 1993). The effects of the combined cropping and digestive constraints on net daily intake are shown in Fig. 3-1 (adapted from Fryxell 1991), which indicates the maximum net intake occurs at an intermediate biomass where the two constraints intersect. The hypothesis that energy intake is maximized at intermediate forage biomass (IFB herafter) was coined the ‘forage maturation hypothesis’ (FMH) by McNaughton (1984) and Fryxell (1991). Controlled pasture experiments with red deer (*Cervus elaphus*) (Wilmshurst et al. 1999) and elk (Albon and Langvatn 1992) provide small-scale support for this hypothesis.

Empirical evidence that migratory ungulates select for areas of IFB to maximize energy intake rates comes primarily from savannah ecosystems, where forage growth is driven by seasonal rainfall (McNaughton 1985). Wilmshurst et al. (1999) showed migratory wildebeest in the Serengeti selected for IFB at landscape scales, but once in high quality patches did not select IFB at finer scales, resulting in maximum energy intake rates. In temperate montane ecosystems, forage phenology varies primarily with topographic and elevational gradients that affect snowmelt and the start of plant growth. For example, plant growth is delayed at higher elevations and on north aspects (e.g., Bennett and Mathias 1984, Walker et al. 1993, Kikvidze et al. 2005). Indeed, studies have shown that montane ungulates have higher indices of diet quality when they have access to a gradient of elevations or a diversity of aspects (Oosenbrug and Theberge 1980, Morgantini and Hudson 1989, Sakuragi et al. 2003), and this translates to higher body mass (Mysterud et al. 2002). To date, there have been no direct tests of whether this results from selection for IFB, in part, because of the difficulties of quantifying plant biomass of mixed communities (e.g. herbs and shrubs) at the large scales that ungulates use in spatially complex mountainous environments (e.g., Merrill et al. 1995). Further, because of the topographic complexity in mountain ecosystems, ungulates may also select for IFB at multiple scales (Boyce et al. 2002).

In this paper, I examined patterns of multi-scale selection for forage biomass by elk to test the forage maturation hypothesis (FMH) in a partially migratory elk population in the Canadian Rocky Mountains. Partially migratory populations, where some individuals migrate and others are resident year round, largely have been overlooked in the study of montane migration (but see Nicholson et al. 1997, Ball et al. 2001). Yet, these systems provide a powerful comparative and theoretical (e.g. Kaitala et al. 1993) framework to test for the population consequences of forage selection differences (Kaitala et al. 1993). I start by examining whether the necessary trade-off between forage biomass and quality occurs across plant communities in this study area (e.g., Fryxell et al. 1991). Second, I modeled the spatial and temporal patterns in forage biomass and quality using a combination of ground sampling and remote sensing approaches to understand differences between migrant and resident summer ranges. Third, I evaluated whether radiocollared elk selected for areas with IFB at four spatial-scales (e.g., Johnson 1980): across the study area, within the summer range, along the movement path, and in the diet (Fig. 3-2). I hypothesized that migration was associated with strong selection for IFB at large scales related to delayed plant growth, whereas resident elk selected for intermediate biomass at finer spatial scales (Fig. 3-2). To examine the consequences of these different scales of selection, I compared the *exposure* of migrant and resident elk to digestible forage based on elk locations, predicting that migrant elk would have higher and longer exposure to greater digestible forage than residents. Finally, because exposure, as measured by telemetry locations, may not reflect actual intake, I compared diet composition and fecal nitrogen concentration as an index to diet quality (Fig. 3-2).

STUDY AREA

The study area included the front and main ranges on the eastern slopes of the Canadian Rocky Mountains in and adjacent to Banff National Park (BNP, 51'30'' / 115'30''), and was defined by the movements of the Ya Ha Tinda (YHT) elk herd over a 6,000km^2 area (Fig. 3-3). Elevations range from 1600m in valley bottoms to 3500m. Climate is cold continental, and strongly influenced by the North Pacific Oscillation (Trenberth and Hurrell 1994). The study area is dominated by pronounced east to west gradients in elevation, precipitation, and topographic complexity, all of which are greater in the western part of the study area (Holland and Coen 1983). Growing degree-days and growing season are reduced at higher elevations and in the main ranges of the study area due to later snowmelt and reduced temperatures (Holland and Coen 1983).

Vegetation is classified into three ecoregions: montane, subalpine, and alpine. The montane ecoregion offers prime elk winter range and is dominated by lodgepole pine (*Pinus contorta*) interspersed with Engelmann spruce (*Picea engelmanii*)–willow (*Salix* spp.), aspen (*Populus tremuloides*)–parkland, and grasslands. The principle winter range for this elk herd is the Ya Ha Tinda (YHT) range, located outside of BNP along the Red

Deer River (Fig. 3-3). The YHT is dominated by rough fescue (*Festuca campestris*) grasslands, mixed with trembling aspen, open conifer forests, and willow–bog birch (*Betula glandulosa*) shrublands. Subalpine and alpine ecoregions are comprised of Engelmann spruce–subalpine fir (*Abies lasiocarpa*)–lodgepole forest interspersed with willow–shrublands, subalpine grasslands, and avalanche terrain, grading to open shrub–forb meadows in the alpine ecoregion (Holland and Coen 1983). The study area contains ~200 km^2 of prescribed fires from 1970 as a result of Parks Canada fire restoration policy (White et al. 2003), with the exception of one accidental human caused fire in 2001. Forage biomass for elk is strongly enhanced by fire in the study area (Sachro 2002).

Elk are the most abundant ungulate, numbering 1500-2500 (Holroyd and Van Tighem 1983, Woods 1991). The YHT elk herd is partially migratory; elk leave the winter range in late May and early June and return from late September to December (Morgantini and Hudson 1988, Chapter 1). Most migrants (~90%) move into BNP and the main ranges during summer (Fig. 3-3, Morgantini and Hudson 1988, Chapter 2), providing geographic strata to group migrant and resident summering areas. Accordingly, I consider the main ranges within BNP and the front ranges in the province of Alberta, as migrant and resident ranges, respectively (Fig. 3-3). Although elk are the dominant ungulate, white-tailed deer (*Odocoileus virginanus*), moose, mule deer (*O. hemionas*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and a remnant herd of 5-8 mountain caribou (*Rangifer tarandus*) also occur. Elk are the most important prey for the area's predators, comprising 40-70% of wolf diet (Hebblewhite et al. 2004) and are important to grizzly bear (*Ursus arctos*) diet (Hebblewhite et al. 2004). Other less important carnivores for elk (Chapter 5) include black bears (*Ursus americanus*), cougars (*Felis concolour*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*).

METHODS

Forage biomass-quality relationships: the forage maturation hypothesis

An assumption of the forage maturation hypothesis (FMH) is that availability of highly digestible forage, or digestible energy, is maximized at intermediate forage biomass (IFB). I determined the relationship between forage biomass and forage quality, measured by dry matter digestibility (%DMD)(Van Soest 1982) to determine whether this relationship held for the plant communities in the study area. All herbaceous species were considered as potential forage for elk because elk are herbaceous generalists (Cook 2002, Appendix 2, unpubl.data). In contrast, only the 13 species of shrubs known to be consumed by elk in this study area (Cook 2002, Appendix 2, unpubl.data) were considered as available shrub biomass. This was because some non-forage shrubs, especially *Betula glandulosa* which is not eaten by elk (Cook 2002, Sacharo 2005), comprised >60% of available biomass in some landcover types (Appendix 2).

Forage growth

I estimated changes in forage biomass and quality over the growing season by repeatedly sampling 30 vegetation sites each month, for a total of 255 times (3.4 times/site/season) from 1 May (or after snowmelt) until 1 October 2002-2004. Sites were stratified by key phenological variables, including open/closed-canopied vegetation types (defined in Table 3-4), low/high elevation, three topographic aspect classes, and by the front and main ranges of the Canadian Rockies (Appendix 2). During each sampling period, total herbaceous forage biomass (g/m^2) was indirectly estimated within ten 0.25-m^2 quadrats from the height of a disc-pasture meter (Dorgeloh 2002) and a disc height-total biomass regression model (Appendix 2). The predicted total herbaceous biomass from the disc-height regression model was converted to green biomass using % green cover estimates (Appendix 2). Percent cover of green and standing herbaceous biomass was estimated visually. Values were averaged across the 10 quadrats to obtain one herbaceous biomass estimate per site and sampling occasion.

The growth of shrub biomass was estimated in both 2002 and 2003 at each repeat sampling occasion using an indirect approach. At each site, the leaf and twig biomass (g/m^2) at the peak of the growing season was estimated as the product of stem density (#stems/0.25m^2) and biomass/stem (g/stem) measured in 3 quadrats/site. Biomass/stem of each shrub species was estimated from functions for leaf and twigs (< 0.7mm) from basal diameter using allometric equations derived by Visscher et al. (2006): see Appendix 2 for details. Peak leaf and twig biomass was adjusted separately by adjusting both by the % of maximum leaf and twig biomass during each time period. Percent change in leaf and twig biomass was based on estimates of percent of maximum leaf and leaf length measured on 5 twigs/shrub species in 3 quadrats/site (n=15/site), and averaged by time period. Current annual growth (CAG) of twigs and leaf lengths was recorded on average for ~32 twigs and 36 leaves per sampling occasion (Appendix 2).

Forage quality

Dry matter digestibility was determined for the top 72% of species (n=64) consumed by elk including shrubs (Appendix 2) by collecting 10-20 plant samples/species >2cm height (i.e., edible by elk) for analyses in each of 4 phenological classes from at least 4 sites across the study area (total n=384 samples). Plant samples were collected from a general area within a site (4-5 ha), and combined individual plants into one composite sample/site, which was subsequently dried at <60° C for 24 hr. Samples were analyzed using detergent fiber analysis (Hanley et al. 1992) at the University of Guelph. For the 24 species (Appendix 2) known be high in tannins, samples were also analyzed using a Bovine Serum Assay (BSA) at the Wildlife Habitat Nutrition Laboratory at Washington State University to estimate digestive inhibition due to tannins. Crude protein was analyzed using the Kjeldahl method (Van Soest 1982). DMD was estimated using predictive summative equations accounting for tannin-induced digestion inhibition (Robbins et al. 1987a,b, Hanley et al. 1992). First, the % digestible protein was adjusted for tannin inhibition using:

$$\%\ \text{Digestible Protein (DP)} = -3.87 + 0.923{*}\text{CP} - 11.82{*}\text{BSA} \quad (4)$$

where CP = crude protein content (6.25 x total N) and BSA indexes the inhibition caused by increasing tannins in mg/mg of dry matter forage, measured using BSA precipitation (Hanley et al. 1992). DP was then used to adjust DMD:

$$\%\text{DMD}=[(0.923e^{-0.045{*}\text{ADL}} -0.03{*}\text{AIA})(\text{NDF})] + [(-16.03+1.02{*}\text{NDS})-2.8{*}\text{DP}] \quad (5)$$

where ADL is the % acid detergent fibre (ADF) that is lignin and cutin, AIA is the biogenic silica content of monocots in %, NDF is the neutral detergent fibre, NDS is the neutral detergent solubles, and DP is the % reduction in protein digestion (the 11.82 *

BSA term in Eq. 4). For non-tanniniferous species the BSA precipitate was assumed to be =0 and thus ignored in the –2.8*DP term in Eq.4.

To calculate an average DMD in each site for each repeat-sampling period, the average % species cover from the ten 0.25m^2-quadrats was recorded for herbs and shrubs during each sampling occasion in four phenological classes: old growth, newly emergent, matured (included fruiting/flowering, and mature growth), and cured. The weighted average DMD was calculated for each site based on % cover in each phenological stage for each species, and species-specific forage quality estimates calculated above. Forage quality estimates were available for 72% of all species eaten by elk (see results). However, I ignored the contribution of the rarest species in the diet because these individual species constituted, on average <1% of the diet/species (unpubl.data).

Forage quality-quantity relationship

The relationship between forage quality (%DMD) and quantity (g/m^2) was estimated separately for herbaceous and shrub biomass using linear and non-linear regression. Forage quality–quantity relationships were estimated for: (a) the entire growing season, (b) for 16-day intervals during the growing season, and (c) spatially between the front and main ranges of the Rockies for the same time period.

Dynamic model of seasonal forage biomass

The spatio-temporal dynamics of herbaceous and shrub biomass available to elk was modeled across the study area from 1 May 2002 to 30 October 2004, using a combination of empirical and remote sensing approaches. First, the total herbaceous and shrub biomass was modeled at the peak of the growing season. Second, total herbaceous and shrub biomass was adjusted for forage growth over the growing season every 16 days using different approaches for closed or open-canopied habitats.

Peak forage biomass

Forage biomass (g/m^2) at the peak of the growing season was statistically modeled within a landcover map derived from a supervised classification of LANDSAT TM imagery at a spatial resolution of 30m^2 (Franklin et al. 2001, McDermid 2005,). Landcover types included: closed conifer, moderate conifer, open conifer, shrublands, upland herbaceous, mixed forest, deciduous, water, and rock/ice (see Franklin et al. 2001 for details). The landcover classification was expanded to include fires in three vegetation types (forest, grassland, and shrub) within 4 age classes (0-1, 2-4, 5-15, >14 years) for 12 burn types (Appendix 2, Sachro 2002). Because of the importance of alpine ranges to elk (Morgantini and Hudson 1989), alpine meadows and shrublands were delineated using an elevation cut of 2200m (Holland and Coen 1983). Cutblocks and salvage logged burns were important in the eastern part of the study area, and a cutblock cover type and 2 age-classes of salvage-logged burns were therefore included (Munro et al. 2006).

Peak forage biomass was sampled randomly following a proportional allocation design (Thompson 1992) within strata designated by landcover type, fire age-classes, slope, and aspect classes (Appendix 2). Between July 2-Aug 28 of 2001-2004, 983 peak of biomass sites were sampled for a sampling intensity of 0.16 sites/km^2. Average sampling date was July 29 (JD= 211, Stdev=12.8), and there was no effect of sampling date on biomass (Appendix 2). At each site, plant cover was estimated within three 0.1m^2 (2001) or five 0.25-m^2- quadrats (2002-2004) systematically placed along a 30-m transect and clipped total (green + standing dead) herbaceous biomass in three quadrats, which were averaged for one biomass estimate/site. Wet mass of forage biomass was weighed in the field; in the lab dry weight was obtained from n=599 samples oven dried at 50°C for 48 hours. Wet weights were converted to dry weights based on conversion ratios for each plant class when oven drying was not possible (n= 384)(Appendix 2). Total shrub biomass was estimated during 2002-2004 (not 2001) using the same approach as described in the forage maturation section above based on basal diameter–biomass relationships (Appendix 2, Visscher et al. 2006). Shrub biomass was converted to biomass of only forage species and leaf-forage biomass (g/m^2) using mean % conversions for both within each landcover types (Appendix 2).

I developed predictive statistical models for forb, graminoid, and total shrub biomass (g/m^2) at the peak of the growing season as a function of spatial covariates (see Anderson et al. (2005) for a similar approach). Spatial covariates were measured at $30m^2$ resolution and included: landcover class, year, 3 aspect classes (north, 0-112.5^o and 292.5-360; south, 112.5-292.5; flat), hillshade (0 to 254, indexing xeric sites with high solar incidence), a soil drainage index (5.3-29.3, indexing the area draining into a pixel), slope (in degrees), elevation (m), greenness vegetation index derived from an Aug 1998 LANDSAT thematic mapper satellite image (Stevens 2002), and distance to the continental divide in km (see Appendix 2 for more details on covariates). Covariates were screened for collinearity using a criteria of $r<0.5$ and variance inflation scores <1 (McCullough and Nelder 1989). Forb and graminoid biomass was modeled using generalized linear models (GLM) with the log-link appropriate to their distribution, and shrub biomass was modeled using the identity link (McCullough and Nelder 1989). Backward-stepwise model selection (McCullough and Nelder 1989) was used instead of an information theoretic approach because of the difficulty in selecting meaningful *a priori* models and because prediction was the goal (Guthery et al. 2005, Stephens et al. 2005). For forb and graminoid models, twenty percent of sites were randomly withheld for out-of-sample cross-validation by comparing observed to predicted biomass using Pearsons *r*. Because of reduced sample size for shrubs, model validation was only conducted within sample and the predicted and observed shrub biomass was compared using Pearson's *r*. Predicted forb and graminoid biomass (g/m^2) was mapped for each 30-m^2 pixel from 2001-2004 in ARCGIS 9.0 (ESRI), and subsequently summed to equal total standing (green + dead) herbaceous biomass.

Seasonal forage growth

Seasonal forage growth was modeled by combining different approaches in open and closed-canopied cover types. Only total green herbaceous biomass, not shrub biomass, was used to determine which environmental factors influenced seasonal growth dynamics. Because the normalized difference vegetation index (NDVI) is closely related to actively growing vegetation in open habitats (Tuckers and Sellars 1986, Thoma et al. 2002), NDVI derived from MODIS satellite imagery (Huete et al. 2002) was used to predict forage growth dynamics (open habitats defined in Table 3-4). NDVI data were obtained from MODIS at a 250m^2 resolution in16-day interval composite images from 22 April to 30 October 2004 (http://modis.gsfc.nasa.gov). NDVI-time series were smoothed for each MODIS pixel using a temporal window size of 3 intervals to reduce noise (Kawamura et al. 2005)(see Appendix 2 for details on MODIS data processing). For each 16-day interval, *i*=1 to *n*, the ratio of the $NDVI_i$ for time period *i* to the maximum $NDVI_{max}$ observed during the growing season was calculated for each 250m^2 pixel, e.g.,

$NDVI_i$ / $NDVI_{max}$. This ratio, which represented the % of maximum forage growth, was then multiplied by the predicted vegetative biomass at 30 m^2 for each 16-day interval to generate a time-series of n=12 forage biomass 'maps' for each growing season.

The above approach makes three assumptions. First, it assumes that herbaceous biomass and NDVI were correlated (e.g., Thoma et al. 2002). This assumption was tested using linear regression of NDVI values for each interval *i* against temporally matched, ground estimates of (a) green herbaceous, (b) standing dead, (c) forb and (d) graminoid biomass. I examined the relationship between NDVI and these four biomass components to confirm that NDVI was strongly related to green herbaceous biomass. I clustered linear regression by sites to adjust standard errors for multi-year sampling in sites using the Huber-White sandwich estimator (White et al. 1980), and included basic covariates such as elevation and distance to divide where they improved model fit (*sensu* Thoma et al. 2002). A second assumption is that by using only herbaceous biomass to model growth, shrub and herbaceous growth was assumed to be similar. This assumption was tested using the Pearsons' correlation between the predicted peak of herbaceous forage biomass and peak of leaf and twig shrub biomass (see *Growing season characteristics section below*) for each site. Lastly, my approach to model forage growth assumed seasonal changes in forage growth in 2004 were similar in other years; data to support this assumption are provided below.

In closed-canopied areas, satellite-based measures of NDVI are unrelated to understory forage biomass due to canopy interference (Chen et al 2004). Therefore, forage growth was modeled in closed-canopied areas using data from the 30 repeatedly sampled vegetation sites described above in the *Forage quality-quantity trade-off* section.

I modeled green herbaceous biomass (*Y*) for a 30-m pixel as a quadratic function of sampling date – Julian day (JD), year, and landscape covariates in GLM's (using the identity link) as:

$$Y_{IJK}= \beta_0 + \beta_1(\mathrm{JD}_K) - \beta_2(\mathrm{JD}_K)^2 + \beta_3(\mathrm{YEAR})_{IJ} + \beta_4 X_{4I} + {}_{\ldots} + \beta_N X_{NI} + \varepsilon \qquad (1)$$

where i= sites 1…n, and j= sampling year 1.m, and k= within season sampling time 1.p, and X_{i} were elevation, slope, aspect class, open/closed and distance to continental divide. Backwards-stepwise model selection was used to select the top model, linear regression assumptions were tested, and analyses were clustered on site. The top model was used to predict forage biomass in closed-canopied cover types for the mid-point JD of each time 16-day interval, i=1 to n, as above for MODIS NDVI. The ratio of predicted biomass at time interval i to the maximum value observed (i.e., $\mathrm{Biomass}_i$ / $\mathrm{Biomass}_{max}$) was then used to adjust peak biomass within season.

Combining open and closed canopy forage growth models into a dynamic seasonal forage model

The predicted peak of forage biomass (both herbaceous and shrub, at $30\mathrm{m}^2$) was then multiplied by the appropriate open and closed habitat % of maximum growth model for each 16-day MODIS interval to derive a time series of herbaceous and shrub biomass models for each growing season. Note that peak biomass was modeled at a fine scale ($30\mathrm{m}^2$), but adjusted in open habitats for seasonal growth using NDVI at a larger $250\mathrm{m}^2$–scale. For both open (NDVI) and closed cover (empirical biomass) types, peak total biomass (standing + green herbaceous) was adjusted using only green biomass growth dynamics, assuming standing dead biomass is constant over the growing season. Spatial modeling was performed in GIS using ARCGIS 9.0 (ESRI).

Growing season characteristics

I compared forage growth curves across the study area to understand how large-scale gradients influenced plant phenology and hence forage quality for elk.

Growing season

Individual forage growth curves were estimated for green herbaceous biomass for each of the 30 sites where vegetation was repeatedly measured using GLM's (identity link) of the form:

$$Y_{ijk} = \beta_0 + \beta_1(\mathrm{JD}_{ijk}) - \beta_2(\mathrm{JD}_{ijk})^2 \qquad (2)$$

where i= site $1\ldots n$, and j= sampling year $1.m$, and k= sampling occasion $1.p$. Growing season start and end dates were defined following Jaggoby et al. (2002) as the JD when the predicted biomass curve intersected a growing threshold that was 25% of the difference between the average forage biomass maximum and minimum for each site (e.g., Fig. 3-4). Peak of green forage biomass was estimated by taking the derivative of Eq. 2 with respect to Y for each site, and length of growing season was the difference between start and end. The influence of environmental factors on each of the four phenological parameters was examined using the GLM (identity link):

$$\theta_{\mathrm{IJ}} = \beta_0 + \beta_1(\mathrm{YEAR})_{IJ} + \beta_2 X_{2I} + \ldots + \beta_N X_{NI} + \varepsilon \qquad (3)$$

where θ_{ij} is the parameter of start, end, peak, and length of growing season at site i in year j , and $X_{2.n}$ are the independent variables year, open/closed habitats, north, south, and flat aspects, elevation (m) and distance to continental divide (km) for site i. The best predictive model with the highest r^2 was selected using backwards-stepwise model selection, clustering on sites.

I modeled seasonal shrub growth to test the assumption that herbaceous growth dynamics adequately described shrub dynamics; as a result, I briefly review methods here and only report results pertinent to testing this assumption (See Appendix 2 for more details). Seasonal shrub growth was estimated at repeat sampling occasions as % of maximum of leaf or twig length, measured as described above in the *forage quality-quantity relationships* section above. To model the % of maximum shrub (leaf, twig) growth, shrub growth was first dichotomized as the probability of leaf or twig growth being >0.5 or ≤0.5 complete. This binary variable was then modeled as a function of time (JD, the critical variable for the assumption) and other covariates using backwards-stepwise model selection. For comparison to the peak of herbaceous biomass, I defined the peak of shrub growth as the predicted JD where shrub leaf and CAG biomass = 0.90. This predicted peak of shrub biomass was then compared to the average (across years, because shrub maturation did not differ between years) herbaceous biomass peak date for each site using Pearson's correlation.

Plant phenology

Differences in phenology of forbs, graminoids, and shrubs were tested in the 30 repeatedly sampled sites described in the forage biomass-quality section above. The average % species cover was recorded in 10-quadrats during each sampling occasion in four phenological classes: old growth, newly emergent, matured (included fruiting/flowering, and mature growth), and cured. Following Griffith et al. (2002), each phenology class was assigned an ordinal score of 1= old vegetation, 2=newly emergent, 3= mature, and 4= senesced/cured. The frequency-weighted phenology score was then calculated for each species, and then by site, to derive the median phenology score by sampling date. Median phenology scores indexed younger plant growth, but not necessarily plant quality because old and cured plants would have similar quality, but phenology scores of 1 and 4. Differences in median phenology scores were tested using a 3-factor ANOVA with migrant status, open/closed, and month (May to August) as categorical variables, clustered on sample sites as above (White et al. 1983). Two-way interactions were included, and Bonferonni post-hoc tests were used to test which months and month-interactions were significant (Zar 1995). To test that differences in median phenology scores also translated to real differences in exposure to the most nutritious forage class, the proportion of newly emergent plants was compared between front and main ranges of the Rockies, open and closed canopied areas, and high and low elevations.

Elk telemetry data

Elk were captured during winter (15 Jan to 31 Mar) from 2002-2004 at the YHT where 95% of the elk population winters (U. of Alberta Animal Care Protocol #353112). Most (95%) elk were captured using two corral traps baited with alfalfa hay and live handled without chemical immobilization. The remainder of the female elk (5%) were captured using helicopter netgunning. Female elk (>yearling age) were outfitted with VHF or GPS radiocollars (LOTEK Ltd.). Between 1 May and 31 October annually, both GPS and VHF collared elk were relocated aerially or from the ground on a weekly basis. Aerial telemetry was conducted in a Cessna Skymaster 337; mean location error was 218m (n=20 blind trials). VHF data were screened such that elk had $\geq$10 VHF locations/ summer. GPS collar data were resampled to a 2-hour relocation to keep autocorrelation structure consistent for statistical modeling. The Bessel function was used to model GPS collar error, 50% of locations were within 34m of the true location, and 95% were within 113m (Appendix 3). Habitat-induced GPS bias was low enough with LOTEK GPS collars (<10%, Appendix 3) to not influence habitat analyses (e.g., Frair et al. 2005). I defined migration as movements between non-overlapping seasonal summer ranges (Craighead et al. 1972). Using telemetry data, I defined migrant and summer ranges corresponding to the main ranges of the Rockies inside BNP, and the front ranges surrounding the YHT ranch area, respectively (Fig. 3-3, Chapter 2).

Elk-forage selection at multiple scales

Selection of seasonal ranges within the study area

The decision to migrate or not effectively reflects Johnson's (1980) 2nd-order scale of selection. Thus, both migrants and residents had equal availability of areas to select summer ranges at the scale of the study area. As a result, I contrasted herbaceous and shrub biomass, growing season characteristics, and landscape features influencing plant phenology in seasonal ranges of resident (n=67) and migrant (n =44) elk to compare selection at the scale of the study area. A multi-annual 100% summer range MCP was derived for each elk for 2002-2004 using Hawthtools 3.19 (Beyer 2005). Covariate values for each elk seasonal range were calculated using the zonal statistics function within Hawthtools 3.19 (Beyer 2005). Covariates included: the average elevation (m), distance to the continental divide (km), richness of 100-metre elevation classes and 9-cardinal aspect classes (including flat) surrounding each pixel, herbaceous and shrub biomass on 4 August, growing season length, and start of growing season. Elevation- and aspect-class richness (number of unique values) was calculated within a 1900 metre (m) radius (mean 24-hr movement rate, *unpubl. data*). Average growing season start and length within each MCP were estimated using GIS derivations of Eq. 3 (see *Growing season characteristics section*). Differences in multiple dependent variables between migrant and resident summer ranges were tested using MANOVA (Zar 1995). Then, correcting for multiple-comparisons, a one-way ANOVA was used to test for each covariate to examine the magnitude of the differences (Zar 1995).

Within seasonal range RSF

Elk selection for forage biomass within summer ranges was compared (Johnson's 1980 3rd-order scale) at two levels using resource selection functions (RSF). An RSF is any function that is proportional to the probability of use of a resource unit (Manly et al. 2002). I estimated RSF models using logistic regression to derive parameters. Because the true sampling fraction is unknown in used-available designs, however, the RSF is only a relative function (Manly et al. 2002). While Keating and Cherry (2004) suggested potential problems with relative RSF models, such problems appear unwarranted for typical RSF applications (Johnson et al. 2006).

First, forage selection was examined within summer ranges using the used-available design of Manly et al. (2002) where used locations were compared to available measured using a constant density of 10 random points/km^2 of elk summer range area from the 100% MCP. For time-specific covariates, like forage biomass, values were derived from the appropriate 16-day interval matching the elk location, or at random for the availability sample. Following Manly et al. (2002) the RSF was estimated following

$$\hat{w}^*(x) = \exp(\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_n x_n) \qquad (6)$$

where $\hat{w}^*(x)$ is the relative probability of use as a function of covariates x_n, and $\hat{\beta}_{1..n}$ are the coefficients estimated from logistic regression (Manly et al. 2002).

Second, elk resource selection was analyzed along movement paths (i.e., Compton et al. 2002) using conditional fixed-effects logistic regression, also known as discrete choice or matched case-control models (Hosmer and Lemeshow 2000, Long and Freese 2004). In conditional fixed-effects logistic models, responses (e.g., 0, 1) are paired and contrasted (Long and Freese 2004). In the context of RSF models, the pair is usually a constrained measure of availability (0) for each used (1) location (Manly et al. 2002). Availability was defined for each elk GPS location by generating five random points at a distance equal to the observed step-length between each consecutive location using Hawthools 3.19 (Beyer 2005). Using the conditional logit model, the conditional RSF, $\hat{w}(x_{ij})$, was estimated following:

$$\hat{w}(x_{ij}) = \exp(\hat{\beta}_1 x_{ij1} + \hat{\beta}_2 x_{ij2} + ... + \hat{\beta}_n x_{ijn}) \qquad (7)$$

where $\hat{w}$ is the relative probability of the *j*th resource unit being selected at the *i*th group for covariates x_n, and $\hat{\beta}_{1..n}$ are the coefficient estimates for each covariate. Eq. 7 was estimated using CLOGIT in STATA 8.0 (StataCorp 2002). In Eq. 7, each GPS location represents the *i*th group, at which an elk makes one of *j* choices from the 5 random points. For CLOGIT models *n* was considered the number of groups of matched locations for model selection (Pendergast et al.1996).

I used GPS telemetry locations collected over 2002-2004 from 18 collared migrant elk and 8 collared resident to develop RSF models at both within-range scales. To test the FMH hypothesis, I examined an *a priori* candidate set of models (Appendix 2) for resident and migrant elk separately, and compared linear, quadratic, and the best fitting non-linear fractional polynomial (Hosmer and Lemeshow 2000) functions for herbaceous and shrub forage biomass using AIC_c (Burnham and Anderson 1998). Statistically, the selection for IFB would be demonstrated by a positive quadratic function where the maximum is indicated by taking the derivative with respect to forage biomass, in this case. While assessing elk selection for intermediate biomass, I controlled for the effects of elevation, hillshade, soil moisture, slope and landcover types, but report this in Appendix 2 herein focusing only on testing the FMH. At the home-range scale, clustering (White et al. 1980) on individual elk was used to account for within-elk heterogeneity (Pendergast et al. 1996) for the within summer range RSF. At the path-scale, however, because neither clustering nor random effects can be implemented in conditional logit models, I controlled for unbalanced sample sizes between elk using sample weighting (Pfefferman et al. 2002, STATA 8.0).

RSF model validation

Model validation was used to assess the generality and predictive capacity of the top selected RSF models (Boyce et al. 2002, Vaughan and Ormerod 2005). RSF models derived from GPS data were validated using out-of-sample VHF telemetry data from an independent set of 58 migratory and 43 resident elk. At both scales, the top model was used for the summer and monthly periods to predict the relative probability of use for VHF telemetry locations. The area-adjusted frequency of used VHF locations was then compared with area-adjusted frequency of available predicted probabilities within 10 equal availability “bins”, similar to k-folds cross validation (Boyce et al. 2002). The correspondence between the ranked RSF-availability bins and frequency of predicted

VHF use was compared using Spearman's rank correlation (r_s). Values >0.90 were considered to indicate high predictive accuracy.

Elk forage exposure

Forage exposure is defined as the forage biomass and quality available to elk at telemetry locations. Migrant and resident elk exposure to herbaceous and shrub biomass is compared over time. Expected biomass exposure is then converted to expected forage quality (%DMD) using forage quality-biomass relationships developed in the *forage biomass-quality* section.

Exposure to herbaceous and forage species shrub biomass (in g/m^2 at a $30m^2$ scale) was estimated for telemetry locations of 72 and 47 collared migrant and resident elk (including both GPS and VHF collars), respectively, by matching the location with the corresponding 16-day interval of the dynamic forage biomass model. Differences in herbaceous and shrub biomass exposure between migrant and resident's telemetry locations were tested using linear mixed effects models with individual elk as a random effect (Skrondal and Rabe-Hesketh 2004), and accounting for autocorrelation within elk (Baltagi and Wu 1999). Herbaceous biomass was *ln*-tranformed to satisfy normality assumptions, while forage and leaf shrub biomass was normally distributed (tested with normal p-p plots). I tested for the effect of migratory status, time in the 12 MODIS-time interval, and their interaction using XTREGAR in STATA 8.0 (Baltagi and Wu 1999, StataCorp 2003). Backwards-stepwise model selection was used to select the best model, which was used to interpret differences between migratory strategies during MODIS intervals over the growing season.

The estimated exposure of herbaceous and shrub forage biomass for migrants and residents was converted to digestibility, %DMD (correcting for tannins), using regressions between %DMD and herbaceous biomass for each 16-day interval developed above, and average interval specific mean %DMD for shrubs (because shrub %DMD was unrelated to biomass, see results). For shrubs, %DMD was adjusted for the % of available shrub biomass that was twig and leaf because of differences in twig and leaf forage digestibility. The weighted average %DMD was then calculated based on shrub and herbaceous biomass availability to evaluate the net forage quality differences between strategies.

Diet composition and quality

I determined whether the above patterns in forage exposure reflected expected differences in diet quality observed in plant diet composition fecal nitrogen.

Diet composition

Pellet samples were collected for diet composition analyses during summer 2002. Each sample constituted a composite of 5 individual pellets selected from 10 pellet groups in a 2-5 ha area, stratified by migrant and resident ranges. Fecal plant fragment analysis was conducted at the Wildlife Habitat Nutrition Laboratory (Pullman, WA, USA). Plant species composition was collapsed to the forage class level (forb, graminoid, shrub) for resident and migrant elk. Differences between migrant and resident elk plant composition were analyzed using ANOVA with main effects as migration status, month, and forage class, with all two-way interactions in Stata 8.0 (StataCorp). Percentage (%) was arcsin-square root transformed to meet normality assumptions (Zar 1995). I used Bonferroni post-hoc multiple comparisons with an experiment-wise error rate of $\alpha=0.10$

to test for differences between migratory strategies within a month and forage class, and between months within a forage class for migrants and residents (Zar 1995).

Fecal nitrogen

Migrant and resident fecal nitrogen (FN) was compared from pellets collected during June to August 2004 as an index of diet quality. Only fresh (>50% were <10 minutes old, remainder <2 days which was verified through visual observations) fecal samples were sampled from migrant and resident ranges, and represented composite collections from different individual pellet groups. Samples were immediately dried at 50°C for 48 hours, and later analyzed for nitrogen content at the Wildlife Habitat Nutrition Lab (Pullman, WA, USA). At each collection site, UTM location was recorded, and distance to continental divide were derived from GIS. I tested for the effects of month (June, July, August) and migratory strategy in a two-factor ANCOVA with distance to continental divide as a continuous covariate.

RESULTS

Forage biomass-quality relationships: the forage maturation hypothesis

Digestibility of green herbaceous biomass declined exponentially as biomass increased (Table 3-1, Fig. 3-5a) over the entire growing season, although early in the growing season (<25 June) when biomass was low, there was no, or a much weaker, relationship between biomass and forage quality. There was no difference in the rate of forage quality decline with increasing biomass between the front and main ranges (*P*=0.43), but the front ranges had higher biomass in general (Fig 5a). Digestibility of total shrub biomass (Table 3-1) was a constant function of biomass over the growing season (Fig. 3-5b) and within individual 16-day intervals (Table 3-1). There was a small but significantly higher mean digestibility of shrub leaf DDM ($F_{1,17}$=3.47, P=0.002), but not twig DDM ($F_{1,17}$=0.32, P=0.57) in the main ranges due to phenological differences. In general, DMD was highest for forbs and shrub leaves and lowest for graminoids during almost all phenological stages (Table 3-2). Shrub leaves were consistently (average of 2.7%) higher in DMD than shrub twigs (Table 3-2).

Dynamic model of seasonal forage biomass

Peak forage biomass

At the peak of the growing season, average total herbaceous biomass ranged from 11.6 g/m^2 in closed conifer to 82.1 g/m^2 in burned shrublands during the study (Table 3-4), but mean biomass was extremely variable (Table 3-3). Open-canopied habitats had almost double the amount of herbaceous biomass (62.5 vs 33.3 g/m^2, Table 3-4), but half as much shrub biomass as closed-canopied habitats (84.2 g/m^2 vs. 163.4 g/m^2, Table 3-4). Forb biomass was highest in 2-year old burns, shrub, and grasslands, while it was moderate in deciduous, mixed forest, and open conifer habitats (Table 3-4). Forb biomass was equally low in closed conifer (the reference type), alpine herbaceous, cutblocks, moderate conifer, new burns (age 0-1) and in salvage logged sites (Table 3-4). In contrast, graminoid biomass was highest in deciduous, burned areas >2 years old, cutblocks, grassland, shrublands, and salvage logged sites, moderate in alpine herbaceous and mixed forest, and lowest in closed/moderate conifer, and new <1 year old burns.

Herbaceous biomass (forb + graminoid) in 2004 was higher than in 2002 and 2003, which were similar (Table 3-3). Large-scale gradients in elevation and distance from the continental divide influenced forb and graminoid biomass, respectively, such that herbaceous biomass declined at higher elevations and closer to the divide. Shrub biomass did not respond to these large-scale gradients, but was higher in areas of higher soil moisture and lower on drier, southwest facing slopes (Table 3-3). Biomass of all three forage components was also correlated with August greenness values (Table 3-3), indicating a close correspondence between NDVI and biomass in this study area.

Peak of forage herbaceous biomass models performed better than the shrub model (Table 3-3). The final models explained 31 and 33% of the variance in forb and graminoid biomass (Table 3-3). Predicted and observed biomass was correlated for forbs (Pearson's $r_{\text{training set}}$=0.53, P<0.005, $r_{\text{test set}}$=0.55, P<0.005) and graminoids (Pearson's $r_{\text{training se}}$=0.56, P <0.005, $r_{\text{test set}}$=0.56, P<0.005). The total shrub biomass model explained only 15% of the variance in total shrub biomass (Table 3-3), and within-sample model validation showed weaker support for predictive capacity (Pearsons r_{all}= 0.37, P<0.001), as might be expected given the extreme standard deviation of forage shrub biomass (Table 3-4).

Seasonal forage growth

Few differences occurred between years in forage phenology (see *Growing season characteristics* below), and as a result I used the NDVI from 2004 to model changes in forage growth in open-canopied areas during the growing seasons of 2002-2004. In open habitats, NDVI in 2004 was most related to green herbaceous biomass (r=0.65, P=0.0008) followed by forb biomass (r=0.60 P=<0.0005), total herbaceous biomass (r=0.58, P=<0.0005), and graminoid biomass (r=0.47, P=0.021; see Appendix 2 for linear regressions). Standing dead biomass was unrelated to NDVI (r=0.28, P=0.08). NDVI, elevation, and distance to continental divide explained the largest portion of the variation in total forage biomass (75%), total green biomass (65%), graminoid biomass (54%) and forb biomass (45%).

In closed-canopied sites, herbaceous biomass peaked at JD= 220 (7 August), and was higher in open-canopied habitats, south aspects, and lower at higher elevations and on more xeric slopes (see Appendix 2 for more details). There were no significant year effects on herbaceous growth and the following top model ($F_{6,24} = 16.2$, $P<0.0005$, n=30) explained 57% of the variation in herbaceous biomass in the repeat sample sites:

$$\text{Herbaceous biomass } (\text{g/m}^2) = 37.7 + 1.90*(\text{JD}) - 0.0043*(\text{JD})^2 + 39.6*(\text{Open}) - 0.10*(\text{Elevation}) + 20.3*(\text{South}) - 0.20*(\text{Hillshade}) \quad (8)$$

Using Eq. 8, I predicted herbaceous biomass at the mid point JD for each 16-day interval for each closed canopy pixel. Where predicted biomass was <0 g/m^2, such as at high elevations early and late in the growing season, the value was set to 0 g/m^2, which functionally allowed biomass estimates at the start and end date of the growing season to vary because biomass declined with increasing elevations (Table 3-3).

Growing season characteristics

Growing season

Mean growing season start date was JD=124, or 3 May, and the top model explained 50% of the variation (Table 3-5). Start dates were not different between any years of the study, confirming similar phenology in start date. The growing season started 2.2 days earlier every 1 km east of the continental divide (Table 3-5), and was delayed by almost 50 days for every 1000-m elevation gain. Start of the growing season was 8 days earlier on south relative to flat and north aspects, and 17 days earlier in open habitats (Table 3-5). Mean peak of forage biomass occurred on 3 Aug (JD=216). The linear regression model for peak date explained 28% of the variance in peak date (Table 3-5). Forage biomass peaked 17.2 days later on north aspects, and 8.3 days later on south relative to flat aspects, although south aspects were variable (Table 3-5). Biomass in open canopied habitats peaked 12 days later than closed canopied habitats. The only year that differed phenologically in terms of the peak of the growing season was 2004, which peaked 10.6 days later than 2002 or 2003. Notably, elevation and distance to the continental divide did not influence the date of peak growth, indicating that despite spatial differences in start dates, growth peaked consistently across the study area. Most sites had not crossed the growth threshold by 15 October of each year (71% of sites). The best model explained 51% of the variance in growing season length (Table 3-5). Growing season length increased by ~1 day for every 2 km east of the continental divide and decreased almost 54 days with every 1000m-elevation gain. Growing season length was almost 22 days longer in open habitats compared to closed, but was 14 days shorter on north facing aspects compared to flat or south aspects (Table 3-5). Finally, the best end-of-growing season model predicted a constant end to the growing season of JD=283, or approximately 9 Oct (Table 3-5). No other covariates influenced end of growing season date. Average growing season length was 157 days, or ~5.3 months.

Shrub biomass growth models are presented in Appendix 2. Herein, I used the predicted peak of shrub and leaf biomass from logit models for comparison to herbaceous forage growth to test my assumption about herbaceous and shrub biomass being equivalent. Leaf biomass peaked in close correspondence to herbaceous biomass (r=0.50, p=0.001); peak Julian date of leaf growth ($\bar{x} = 210$) was close to average herbaceous peak date ($\bar{x} = 212$). Date of predicted twig peak growth was correlated to herbaceous biomass (r=0.45, p=0.03), but delayed, peaking approximately 46 days later ($\bar{x} = 258$) than herbaceous biomass ($\bar{x} = 212$) within a site, indicating continued growth.

Species phenology

The best model for predicting the median phenology score of shrubs forb ($F_{9, 18}$= 62.8, *P*<0.00005), graminoid ($F_{11,18}$=573.1, *P*<0.00005), and shrub ($F_{6,19}$=69.1, *P*<0.0005) explained 71%, 49%, and 56% of the variance, respectively. Main ranges had consistently lower median phenology-scores (e.g., delayed growth) than front ranges for forbs (β_{main} = -0.52, *P*<0.0005), graminoids (β_{main} = -1.09, *P*=0.034), and shrubs (β_{main} = -0.15, *P*=0.15), although the difference was non-significant for shrubs.

Phenological differences in graminoids between main and front ranges existed during the entire growing season (Fig. 3-6), but rapidly cured on both ranges in September. Forb phenology was delayed in the main ranges only in June (*P*=0.025) and July (*P*= 0.03), with the difference existing only in open habitats. Finally, shrub phenology scores were the same in open and closed habitats, and between the front and main ranges (Fig. 3-6).

Differences in median phenology scores translated to prolonged duration and higher proportion of newly emergent graminoid and forb biomass in the main ranges compared to the front ranges (Fig. 3-7). At low elevations in the front ranges, the proportion of newly emergent forbs had already peaked by May in open canopied sites, while they peaked in July/August in closed canopied sites (Fig. 3-7a). At high elevations, newly emerged forbs in both open- and closed-canopied sites in the front ranges peaked in May and declined steadily, whereas on the main ranges they peaked in July (open canopied sites) and in August (closed canopied) sites (Fig. 3-7c-d). The percent of newly emerged graminoids at low elevations of the front ranges was most advanced in the open canopied sites and declined rapidly at these sites, while graminoid growth was considerably delayed in the closed canopied sites at low elevation sites. In contrast, at the high elevation sites in the main ranges there was little difference between phenological growth of grasses (Fig. 3-7c) while on the front ranges growth in closed-canopied sites was delayed.

Elk telemetry

During winters 2002-04, 119 unique individual elk were outfitted with 101 VHF radiocollars and 27 GPS collars (9 elk wore both VHF and GPS at different times during the study), of which 80% were adult females (>2.5 years old), 10 % were subadults (<2.5 years) and 10% were yearlings (<1.5 years). Of the 128 elk, 59% were migrant and 41% were resident. At least 10 VHF locations/ summer were obtained from 56 migrants and 44 residents (Table 3-6). GPS collars were deployed on 19 migrants and 8 on residents collecting ~1,545 locations/summer/elk (Table 3-6). During each 16-day interval, an average of 50 VHF locations were obtained from migrants and 41 from residents, or 2 VHF locations/elk/interval (Table 3-6). GPS collars collected ~144 locations/interval/elk, or 9 locations/day (Table 3-6).

Elk forage selection at multiple scales

Selection of seasonal ranges within the study area

Migrant and resident summer ranges differed for all eight landscape covariates (MANOVA $F_{7,109}$=64.74, $P<0.0005$, Wilks λ=0.349) after adjusting for multiple-comparisons (Table 3-7). As predicted under the FMH, migrant ranges averaged 30-40% lower total herbaceous and shrub biomass than residents, were at an average of ~ 266m higher elevation than residents, were much closer to the continental divide, and had higher elevational and aspect richness (Table 3-7). The start of the growing season on migrant ranges was 23 days later and twice as variable (SD = 19.3 vs SD=9.5) than residents (Table 3-7). Likewise, growing season lengths on migrant ranges were shorter (170 vs. 200 days), but, critically, were also twice as variable (SD = 15.5 vs SD=7.5) as residents (Table 3-7).

Within summer range RSF

Because of low model selection uncertainty (all AIC weights w_i>0.85), I only report the top overall summer and monthly models. Both migrants and residents selected for sites of IFB in June to August, but not in September when elk avoided high biomass, by selecting areas of low biomass (Fig. 3-8, Table 3-8). Solving the quadratic selection function for the maximum to determine the intermediate forage biomass 'optimum' revealed migrants selected a maximum of 70g/m^2, whereas residents selected a maximum of 114 g/m^2 (Fig. 3-8, Table 3-8). In open habitats, the predicted probability of use for migrant elk was less than the expected maximum, whereas the predicted relative probability of use for residents was distributed across the range of available herbaceous biomass (Fig. 3-8). Out-of-sample VHF data closely matched predictions of RSF models at the home-range scale. Predictive capacity (r_s) of migrant models were all r_s >0.62, and residents were >0.81, except during September when r_s =-0.06 (Table 3-9).

At the scale of the movement path, the strength of selection for forage biomass was weaker by both migrants and residents (Fig. 3-9). Migrants showed weak and variable monthly forage biomass selection, selecting in June and September for sites with maximum biomass, whereas during July and August selecting for sites where they minimized biomass (Table 3-9). However, across the entire summer, migrants selected for sites of minimum forage biomass, not IFB (Fig. 3-9, Table 3-9). In contrast, resident elk consistently selected for sites of IFB or minimal biomass at the peak of the growing season during July and August (Table 3-9). Solving the quadratic for the IFB maximum showed resident 'intermediate' selection was in fact for a very high (e.g., Table 3-4) herbaceous biomass of 140g/m^2 (Fig 9, Table 3-9). At the home-range scale, r_s in cross validation of migrant models were all >0.62, and residents were >0.81, except during September when r_s =-0.06 (Table 3-9).

Except for September, migrant and resident elk showed similar shrub biomass selection patterns within home ranges. Instead of selecting for intermediate levels of shrub biomass, migrant and resident elk avoided areas of high shrub biomass early in the growing season (June) and selected for sites of high shrub biomass during July and August (Table 3-8). In comparison, during September residents selected sites with maximum shrub biomass. At the path-scale, both strategies followed the same tactic of selecting for the highest shrub biomass over the whole summer, and for all months, except September, when they selected for minimum shrub biomass (Table 3-9). Finally, out-of-sample elk VHF telemetry data provided strong validation of the predictive capacity of RSF models at both scales, with the exception of September models (Table 3-8, 9). At the summer range scale, migrant and resident r_s were all >0.62 except September, where r_s=0.26 and –0.333, respectively (Table 3-8).

Elk forage exposure

Exposure to herbaceous forage biomass (g/m^2) varied among individual elk ($\hat{\sigma}^2_{elk}$ = 6.53), between migratory strategies, and seasonally in each 16-day interval (Fig. 3-10). The top forage biomass model explained about 78% of the total variance (top linear mixed-effects model Wald χ^2=27,687, P<0.00001). Forage biomass exposure was higher for during 2004 (average effect +31.3 g/m^2, SE=1.45; Fig 10a), whereas exposure in 2003 and 2002 were similar. Herbaceous biomass exposure did not differ between migrant and resident elk prior to migration nor after elk returned to the ranch in the fall (Fig. 3-10a). On summer ranges, however, migrants were consistently exposed to 25-40% lower herbaceous biomass (mean biomass reduction for migrants β=-11.5 g/m^2, SE=1.84; P<0.0005). Individual 16-day periods with significantly lower migrant biomass are marked with an * in Fig. 3-10a. The reduced forage biomass exposure of migrant elk translated to consistently higher exposure to forage quality, averaging 5% (range 2-9%) higher forage digestibility (Fig. 3-10b).

Exposure to total shrub (twig + leaf), and leaf-only shrub biomass was similar for both migrants and residents except during August 12 and 28 intervals when migrants had lower shrub exposure, and during both intervals in June when migrants had higher exposure to leaf forage biomass (Fig. 3-10b). Otherwise, shrub exposure was similar for both. The best linear mixed effects shrub biomass exposure models explained less variation than herbaceous models (total shrub $r^2_{overall}$ = 0.26, leaf $r^2_{overall}$ = 0.36), perhaps because of the higher variance in individual elk exposure to shrub biomass (e.g., shrub $\hat{\sigma}^2_{it}$= 11.3, leaf $\hat{\sigma}^2_{it}$=7.2). Digestibility of exposure to shrubs remained similar throughout the growing season for both migrants and residents, slightly higher for migrants during the 11 July interval, but otherwise identical. Combined, the high digestibility of shrubs reduced the magnitude of the difference in exposure to digestible forage for residents, but migrants still had higher digestibility throughout the entire migratory period.

Diet quality

Diet composition

Graminoids were the dominant forage class consumed by both residents and migrants, constituting at a minimum > 50% of the diet (Table 3-9). Diet composition changed seasonally by forage class (*P*<0.0005) as well as by forage class between migratory strategies (*P*<0.06; overall ANOVA $F_{13,76}$=35.84, *P*<0.0005, r^2=0.84). Migrants consumed less graminoids and more shrubs during June and July than residents (Table 3-10), but not during August when both resident and migrant shrub consumption increased to 30% as graminoid consumption declined. Besides this trade-off between shrub and graminoid, composition of forbs was higher for residents in July, but increased over summer for both strategies (Table 3-10).

Fecal nitrogen

Nitrogen concentration of feces (FN) of both migrants and residents declined (Fig. 3-11) over the growing season ($F_{2,32}$=3.77, P=0.04). While FN of migrant elk was always higher than residents (Fig 11), the different was not statistically significant ($F_{1,32}$=1.01, P=0.32) except during the month of July where migrant FN was 15% higher than residents (interaction; $F_{2,32}$=5.63, P=0.008). In addition, FN was lower in the eastern part of the study area ($F_{1,32}$=3.80, *P*=0.05, Fig 11) with FN declining by –0. 8% (SE=-0.04) for every 10 km east of the continental divide.

DISCUSSION

Because climatic and topographic gradients delayed the overall start of plant growth and topographic variation provided higher aspect richness, elk that migrated to summer ranges closer to the continental divide had access to sites of overall lower biomass but high quality forage for longer periods than resident elk. In addition to these large-scale landscape differences, within these summer ranges, migrants selected for intermediate herbaceous biomass in accordance with the FMH. Finally, at the finest scales, migrants continued to avoid high herbaceous biomass along movement paths. Thus for migrants, delayed and more variable phenology combined with lower herbaceous biomass resulted in migrant elk being exposed to higher forage quality over the migratory period than residents. Exposure to higher forage quality was observed at the diet selection level because migrants consumed more high quality forage classes that translated to higher fecal nitrogen during summer. The congruence of migrant elk forage selection across spatial-scales with expectations under the FMH is consistent with the hypothesis that elk were migrating to maximize forage quality (e.g., Fryxell et al. 1988).

In contrast, by staying on winter ranges during summer where forage phenology was more advanced, non-migratory resident elk were exposed to reduced forage quality earlier and for a longer period than migrants. Resident elk effectively selected for maximum, not intermediate herbaceous biomass, as expected under the FMH, avoiding only the highest herbaceous biomass sites in the study area during summer (Fig. 3-8.). The highest herbaceous biomass (200-250 g/m^2) occurred in burns and cutblocks on the eastern fringe of the study area (Table 3-2, Appendix 2, Sachro 2002). While elk selected burns (Appendix 2), sites they avoided with the highest forage biomass values >200 g/m^2 often had very high % standing dead content (Sachro 2002). Therefore, by remaining on phenologically earlier summer ranges, and by selecting maximum forage biomass, residents were exposed to lower overall availability of highly digestible forage. Resident forage quality exposure translated to higher diet composition of lower quality graminoids (because of earlier phenology) throughout the summer, which resulted in lower FN for residents. However, differences in FN between migrant and resident elk were not that large, suggesting residents may have compensated for lower quality by selecting high quality forage at finer scales than investigated, e.g. at the microsite or plant-part level (Hanley et al. 1992; Spalinger et al. 1992). Indeed, residents' relatively high FN with lower consumption of high tannin forages like shrubs supports this hypothesis. While FN is known to be sensitive to high forb and shrub tannin levels (Robbins et al. 1987a), in this study, mean tannin levels for forbs, shrubs and shrub-leaves averaged 0.04, 0.08, and 0.04 mg BSA/g forage (Appendix 2), respectively, lower than other studies (Robbins et al. 1987b), providing more confidence in the comparison of FN between strategies. Despite FN differences, direct behavioural studies, which are difficult with free-ranging elk, would be required to test for fine-scale foraging compensation for foregoing migration. Migrant elk clearly had the nutritional advantage because of landscape gradients in phenology combined with consistent selection for intermediate herbaceous biomass as expected under the FMH. But how did selection for shrub biomass affect exposure to forage quality between strategies?

Residents and migrants did not select intermediate shrub biomass at any scale, because there was no quality–quantity trade-off between shrub biomass and quality. Instead shrub quality was high and relatively constant, and therefore, selecting maximum, not intermediate shrub biomass would maximize forage quality. Accordingly, both migrants and residents selected maximum shrub biomass as expected during the growing season. High digestibility of shrubs partially offset some of the lower % digestibility of resident diets, especially later in the growing season when diet composition similarly confirmed a switch to shrubs in the diet of residents. Shrub leaves, and especially willow was very important to elk in this study, similar to earlier research (Morgantini and Hudson 1988). Willow species were the 3rd most consumed plant by elk during summer by both migrants and residents, comprising ~12% of all diet overall (Appendix 2). While exposure to total shrub did not differ between strategies, migrants had higher exposure to leaf forage biomass than residents during June. For both strategies, 55% of summer shrub diet of willow was willow leaves with higher % digestibility than twig. The inevitable bias against shrub leaves in diet composition studies, similar to forbs (Bartolome et al. 1995) only emphasizes the importance of leaves in the diet. Thus, shrub selection patterns managed to mitigate resident's overall lower exposure to herbaceous forage quality, but the forage quality of migrants' total forage biomass (herbaceous + shrub) exposure was still an average of 4% higher than residents throughout the migratory period.

By foraging on nutritious newly emergent willow leaves (Kudo et al. 1999) during July and August in alpine shrublands, migrants may also benefit by foraging on earlier phenology shrub leaves with reduced tannin content (e.g., Hanley et al. 1987, Happe et al. 1990;). The overall importance of shrubs to migrant elk in this system has important implications for the timing of fall migration. While quality of overall shrub biomass, including twigs, did not decline much during the growing season, lower digestibility of browse during the dormant season would reduce the benefit of shrubs (Hobbs et al. 1981, Baker and Hobbs 1982,). Therefore, fall migration may be triggered by leaf senescence (i.e, drop), which would rapidly reduce the benefit of migration given lower and equal herbaceous forage quality availability by fall between migrant and resident ranges. Certainly, snow falls have been proximally related to fall migration dates, but this evidence suggests from a foraging perspective, balancing reduced forage quality due to shrub leaf drop may be the ultimate cause of fall migration. In comparison to other studies (e.g., Baker and Hobbs 1982), increased consumption of shrubs/willow leaves in summer may be more important than forbs for providing forage quality of migrants in the Canadian Rockies. Both shrub leaves and forbs have similarly high digestibility and thin cell walls that increase breakdown rates (Spalinger et al. 1992). Biases against forbs in fecal plant fragment analyses, however, make firm conclusions about the importance of forbs difficult.

Other seasonal changes in forage availability and elk forage selection confirm the key role of selection for IFB under the FMH in this system. During September, migrants switched from selecting intermediate or minimum forage biomass to maximizing forage biomass exposure, and this occurred at both the within summer range and along movement path-scales. This switch likely reflects decreasing availability of high quality forage due to senescence. Ungulate selection for maximum forage biomass during the dormant season is well documented (e.g, Hobbs et al. 1983, Wallace et al. 2002). In other migratory systems, the end of the growing season is associated with the return of migratory wildebeest to the high forage biomass, low quality, tall-grass savannah's of the Serengeti (Wilmshurst et al. 1998). Often, fall migration following cessation of the growing season can often be more variable than spring migration, where ungulates are constrained by parturition (Chapter 2; Boyce 1989). This highlights the important role that forage senescence has for the timing of fall (post-growing season) migration, a subject that has not received much applied research beyond snowfall, with the focus of migration usually being movements associated with the spring ‘green’ wave. I predict that fall migration occurs as soon as migrant exposure to % digestibility (DMD) equals that of residents.

The way in which I modeled forage quality likely underestimated forage quality exposure for migrants. I assumed a constant forage quality given a particular species and phenological class, regardless of seasonal and spatial variation in forage quality (e.g. Larter and Nagy 2001, Jorgenson et al. 2002, Mutanga et al. 2004). In the Canadian Rockies, forage quality for the same species in a given phenology class would likely increase at higher elevations and western areas following trends in other mountainous regions (Bennett and Mathias 1984, Walker et al. 1993, Walsh et al. 1997, Kudo et al. 1999). Therefore, the 4-5% overall difference in digestibility of total forage biomass exposure was likely conservative.

But how significant, biologically, are ≥5% differences in forage digestibility? Cook et al. (2004) fed captive elk diets of high, medium, and low forage quality during the summer months, and similar winter forage, over several years to investigate consequences of forage quality during summer to elk survival and reproduction. Elk were not constrained by food quantity, as might be expected in the wild during summer, and mean forage digestibility in summer was 55, 59, and 67% between low, medium, and high quality treatments (Cook et al. 2004). These summer differences were sufficient to manifest at the end of the following winter in reduced calf, yearling and adult female weights, reduced pregnancy rates in the low and medium treatments, calf winter survival, and important carry over effects on future reproduction and survival (Cook et al. 2004).

Although their high forage quality treatment (67%) admittedly exceeded the average forage quality available to elk in western North America (Cook et al. 2002), the ~5% difference between their low and medium diets still had important consequences for survival and reproduction (Cook et al. 2004). These results are corroborated in other experimental settings. For example, sheep foraging on summer diets of high quality *Salix* spp. leaves (10% higher digestibility than the control group) in New Zealand experienced higher body weights at the end of the winter, higher pregnancy rates, and higher lambing rates (McWilliam et al. 2005). Based on these studies, the 5-10% differences in summer exposure to digestible forage would be expected to have important population consequences in the Ya Ha Tinda elk herd. Resident elk should have reduced body weight, pregnancy rates, and perhaps survival from foraging costs alone. In Chapter 5, I show mid-winter body weight of resident female calves is lower than migrant calves, and pregnancy rates of residents were lower than migrants. Despite evidence that elk benefited from migration from a foraging perspective, the decline of migrants in this system (Chapter 2) driven by lower adult female migrant survival (Chapter 5) reveals benefits from forage do not determine fitness of migratory strategies in isolation. Elk must balance the benefits of migration from a foraging perspective with the costs of mortality from predation (e.g., Swingland 1980, Nicholson et al. 1997, Testa 2004).

The relative benefits of migration should be influenced by environmental stochasticity in the peak of forage biomass and plant phenology, such as start and end dates of the growing season. For example, costs of foregoing migration could potentially be counteracted over time by the relatively greater variation in peak herbaceous forage biomass experienced by residents remaining on the winter range. Summer rainfall was near 30-year lows during 2002 and 2003 during this study. There was some evidence that peak herbaceous biomass during this study was related to summer rainfall (r=+0.87, p=0.09, n=4, see Appendix 2); high rainfall in 2004 led to the highest observed biomass during the study. This variation in forage biomass may have allowed residents to compensate for reduced quality by the greater biomass in high rainfall summers. Nicholson et al. (1997) showed that while resident mule deer survival was lower in drought years, it increased relative to migrants during years with high precipitation. Thus, resident fitness from a foraging perspective may be more sensitive to environmental stochasticity during summer than migrants. Migrants would on average have higher forage quality under this scenario, but less variable between years.

Environmental stochasticity in phenology could also potentially influence the differences in forage quality between migrant and resident summer ranges. Phenological change is perhaps the most likely channel for the effects of climate change to manifest on ungulate population dynamics (Post and Klein 1999, Post and Stenseth 1999). For example, climate change scenario's for the Rocky Mountains predict increased frequency of high spring precipitation/snowfall (April-May) and potentially drier summers (Scott et al. 2002). High spring snowfalls would delay phenology and migration (Pettorelli et al. 2005a, Appendix 2) resulting in peak lactation demands occurring during adverse forage and climatic conditions, resulting in potential declines in body mass and population size (Pettorelli et al. 2005a,b). It could also increase variation in calving dates, reducing any predation risk reduction arising from synchronous calving (Testa 2004). At a finer scale, however, climate change may differentially affect migrants and residents because of local effects of the 'climatic downscaling' process (Petorelli et al. 2005b). For example, high spring precipitation would manifest as snowfall at higher elevations and closer to the continental divide (Holland and Coen 1983; Luckman and Kavanagh 2000), but as rainfall at the lower elevation winter range, similar to different effects of high NAO on red deer dependent on local elevation effects (Pettorelli et al. 2005b). Moreover, long-term effects of climate are also expected to lead to treeline advance (Luckman and Kavanagh 2000), reducing the area of alpine habitats that elk showed strong selection for (Morgantini and Hudson 1988; Appendix2). Thus, potential effects of climate change may be more detrimental to migrant populations. My ability to model such phenological variation with this dynamic forage model is presently limited, however. Within the three-year study, I found phenology patterns regarding start of the growing season did not vary. The only difference was 2004 which was < 1 full MODIS interval (16-days) later than 2002 and 2003. Future efforts could easily adapt this approach by shifting the growing season start ± 1-2 MODIS interval periods to modeling effects of phenological variation on benefits of migration.

In summary, migrant elk selected intermediate herbaceous biomass in accordance with the FMH to maximize exposure to higher forage quality than residents across spatial scales. Residents instead selected for maximum herbaceous forage biomass, and both resident and migrant switched to shrub biomass during late summer likely to compensate for declines in herbaceous forage quality. As a result of the difference in selection strategies for herbaceous biomass in particular between migrants and residents, resident elk realized ~5% lower forage quality in terms of digestibility than migrants. The magnitude of this differences in forage quality between strategies is predicted to lead to significant differences in elk body mass, reproduction, and survival (Cook et al. 2004).

Combined with results of previous studies of montane ungulates (Osenbrug and Theberge 1991, Albon and Langvatn 1992, Mysterud et al. 2001, Pettorelli et al. 2005b), the intermediate forage maturation hypothesis (Fryxell et al. 1991) appears to be the mechanism driving elk migration in mountainous ecosystems during the growing season. How migrant and resident elk balance their forage selection against risk, and whether the bottom up effects of higher forage quality manifest in population dynamics of migrant elk remain to be tested.

Table 3-1. Quality-quantity trade-off linear regression models between herbaceous forage biomass (X_1) and % digestibility (Y), and the constant (β_0), or average shrub % digestibility for leaves and twigs for each 16-day Modis interval, and an overall comparison between linear and exponential models for the herbaceous quality-quantity trade-off over the entire growing season.

	β_1 (SE)	β_0 (SE)	N	F	*df*	P	R^2	Mean shrub % DMD-leaf		Mean shrub% DMD-twig	
								M	R	M	R
Modis interval linear model											
May 8	-0.45 (0.24)	54.7 (14.4)	13	3.5	7	0.1	0.25	70.8	68.6	66.8	64.0
May 24	-0.12 (0.13)	39.6 (8.9)	11	0.5	9	0.5	0.05	70.5	69.8	65.8	65.6
Jun 9	-0.09 (0.06)	39.0 (5.5)	27	2.3	25	0.12	0.09	71.1	70.7	66.3	66.9
Jun 25	-0.10 (0.03)	35.6 (3.4)	28	11.9	26	0.02	0.17	72.2	70.5	66.5	66.9
Jul 11	-0.13 (0.05)	39.0 (4.3)	41	7.6	25	0.01	0.25	71.8	69.7	66.9	65.4
Jul 27	-0.10 (0.05)	54.7 (4.7)	26	3.6	13	0.07	0.11	69.5	70.6	64.7	66.0
Aug 12	-0.10 (0.05)	37.5 (3.3)	42	3.9	28	0.05	0.15	68.6	69.0	63.6	63.6
Aug 28	-0.18 (0.05)	36.0 (3.8)	26	14.1	19	0.001	0.39	67.2	67.0	63.0	62.9

	β_1 (SE)	β_0 (SE)	N	F	*df*	P	R^2	Mean shrub % DMD-leaf		Mean shrub% DMD-twig	
								M	R	M	R
Sep 13	-0.33 (0.06)	39.8 (2.5)	9	37.0	7	0.005	0.7	67.1	66.7	63.1	63.8
Sep 29	--	--	1	--	--	--	--	--	--	--	--
Annual herbaceous linear and exponential model											
Linear model	-0.12 (0.03)	38.1 (2.6)	224	15.7	33	0.001	0.18	69.9	69.2	65.2	65.0
Exponential	β_0	β_1	β_2	N	F	*df*	P	R^2			
model $Y=\beta_0+\beta_1*\beta_2X_1$	19.26 (5.50)	22.86 (4.564)	0.96 (0.008)	224	24.06	33	<0.001	0.22			
Exponential model $\Delta AIC_c = 0.00$ Linear model $\Delta AIC_c = 6.51$											

Notes: There was no significant linear or non-linear relationship between shrub % DMD either for leaf or twig and biomass, so the constant is reported. Note *df* is df_2; df_1=1 for all models.

Table 3-2 Average % dry matter digestibility (DMD) for five phenological stages for forbs, graminoids, and shrubs, including twigs and leaves during growing season 2004.

	Forb			Grass			Shrub- Twig			Shrub - Leaf		
	%DMD	N	StDev	%DMD	N	StDev	%DMD	N	StDev	%DMD	N	StDev
New	66.1	55	6.7	61.5	25	9.8	66.4	19	4.9	71.2	6	5.9
Flower	65.0	40	8.1	54.5	13	4.8	68.3	9	3.1	69.6	6	4.9
Fruit	61.6	33	8.9	47.7	24	8.1	59.5	14	6.7	71.4	3	5.4
Mature	62.9	48	9.1	48.3	22	6.1	63.7	17	9.1	65.4	3	8.5
Cured	46.7	18	9.8	38.7	29	6.2	58.0	---	---	---	---	---
Mean	63.4			48.8			63.1			65.9		

Notes: % DMD calculated following methods of Hanley et al. (1992) accounting for tannin digestion inhibition of forbs and shrubs. See text for details.

Table 3-3. Top forage biomass component statistical models predicting forb, graminoid, and total shrub biomass at the peak of the growing seasons, 2001-2004, eastern slopes of BNP, Alberta.

	Forb†		Graminoid‡		Total Shrub††	
F	$F_{18,\,711}=25.26$		$F_{20,699}=21.02$		$F_{21,\,574}=2.72$	
P-value	<0.00005		<0.00005		<0.0001	
R^2	0.31		0.33		0.16	
Parameter	β	SE	β	SE	β	SE
Intercept	0.079	0.429	**1.605**	0.601	**-289.86**	130.17
Elevation	---	---	**-0.001**	3E-04	---	---
Dist. to divide (km)	**0.006**	0.002	---	---	---	---
Wetness	-0.032	0.018	---	---	13.41	6.766
Hillshade	---	---	---	---	-0.94	0.518
Greeness-August	**0.219**	0.045	**0.301**	0.051	**69.31**	13.408
2002	**0.292**	0.149	**-0.362**	0.166	---	---
2003	0.246	0.128	**-0.488**	0.137	---	---
2004	**1.647**	0.126	0.21	0.161	---	---
Alpine shrub	**0.734**	0.243	**0.846**	0.34	**-107.74**	17.516
Alpine herb	---	---	0.537	0.282	**-21.44**	8.067
Deciduous	0.507	0.307	**2.072**	0.24	---	---
Forest regen.	---	---	**1.822**	0.223	**-46.37**	13.571
Grassland	**0.777**	0.166	**1.249**	0.191	**134.08**	13.882
Mixed forest	0.627	0.456	0.593	0.351	**114.68**	11.488
Moderate conifer	---	---	---	---	**63**	10.633
	Forb†		Graminoid‡		Total Shrub††	

Parameter	β	SE	β	SE	β	SE
Open conifer	**0.537**	0.17	**0.615**	0.202	**218.94**	13.855
Shrub	**0.658**	0.155	**1.23**	0.179	**193.16**	16.119
Burned grass 0-1yr	---	---	---	---	**-132.55**	17.923
Burned grass 2-4	**1.163**	0.19	**1.934**	0.214	**-106.1**	19.23
Burned grass 5-14	**1.489**	0.227	**0.992**	0.3	---	---
Burned shrub 0-1	---	---	---	---	**-320.59**	28.86
Burned shrub 2-4	**0.688**	0.226	**1.855**	0.255	**156.07**	12.906
Burned shrub 5-14	**1.067**	0.338	**2.223**	0.372	**-62.34**	16.488
Burned forest 0-1	---	---	---	---	**-102.08**	8.432
Burned forest 2-4	**0.763**	0.175	**1.074**	0.229	**-80.79**	10.25
Burned forest 5-14	**1.016**	0.212	**1.099**	0.227	---	---
Salvaged 2-4	---	---	**1.267**	0.277	**-64.97**	7.779

Notes: Bolded coefficients are significant at P=0.05. Blanks cells did not significantly differ from the reference category, which was closed conifer for all 3 models with the exception of burned habitats. Burned habitats were dummy coded for GLM models such that the statistical comparison was with the unburned reference habitat of that burn type. For example, burned forest 5-14 years old for shrubs was not different than closed conifer. See text for details.

† Forb biomass was ln-transformed.

‡ Graminoid biomass was ln-transformed.

†† Total shrub biomass (leaf and twig) was untransformed.

Table 3-4. Mean total herbaceous and forage spp. shrub (leaf and twig) biomass at the peak of the growing season (Aug 4) for the 14-landcover types used in the study, from 2001-2004, with total number of plots sampled and standard deviation.

Cover Type	N	Herbaceous	SD	Shrub	SD
Alpine-herbaceous *	28	21.2	17.94	84.3	252.42
Alpine-shrubs*	25	34.6	21.47	83.2	180.08
Burn-forest*	186	69.4	60.72	65.5	160.20
Burn-grassland*	64	78.5	70.44	42.9	135.73
Burn-shrub*	49	82.2	68.93	137.9	422.60
Salvage*	60	62.8	61.21	70.9	202.11
Closed conifer	55	10.6	11.67	161.8	361.58
Deciduous	10	79.2	42.66	98.6	133.53
Cutblocks*	16	63.5	23.96	54.9	281.95
Herbaceous*	92	79.5	45.33	102.3	364.28
Mixed forest	13	32.6	36.28	212.7	439.83
Moderate conifer	188	20.9	24.31	116.2	399.96
Open conifer	88	33.4	30.63	231.1	442.84
Shrubs*	106	70.3	55.74	115.6	515.79
Total/Mean	980	$\bar{x} = 50.6$		$\bar{x} = 144.2$	

Notes: * indicates open habitat used in forage modeling, see Appendix 2 for canopy closure definitions.

Table 3-5. Summary table of top forage growth models for the eastern slopes of BNP, during the growing seasons 1 May to 15 October, 2002-2004. Shown are details for the top models and parameter estimates with associated robust standard errors.

Model Fit	Start of Growing Season	Date of Peak of Forage Biomass	End of Growing Season	Length of Growing Season
F	$F_{4,19}=22.12$	$F_{4,26}=5.49$	$F_{0,24}=0.01$	$F_{4,24}=11.71$
P-value	$P<0.00005$	$P=0.0024$	--	$P<0.00005$
R^2	0.59	0.28	--	0.51
<u>Variables</u>				
Intercept β_0	65.5 (17.11)	196.6 (5.88)	281.6 (1.79)	262.6 (24.29)
Dist. Divide (km)	-0.45 (0.095)	---	---	0.59 (0.181)
Elevation (m)	0.051 (0.008)	---	---	-0.054 (0.010)
Open	-16.7 (4.53)	12.8 (4.37)	---	22.9 (7.02)
North Aspects	---	17.2 (6.28)	---	-14.1 (5.55)
South Aspects	-8.0 (4.25)	8.3 (6.29)	---	---
Year 2004	---	10.7 5(.89)	---	---
Year 2003	---	---	---	---

Notes: Models were estimated clustered on individual plots across years to reduce autocorrelation. Reference categories for the intercepts of models are: a) for the date of peak, flat closed habitats during 2002 and 2003, b) for the start of growing season, flat and north facing closed habitats, c) for the end of growing season, flat/south closed habitats, and d) for season length, closed south and flat habitats.

Table 3-6. Telemetry data for migrant and resident VHF and GPS collared elk during summers 2002-2004, YHT elk population used for estimating forage exposure (May-October) and resource selection functions (RSF's, June-September), BNP, Alberta.

Strategy	Data	Metric	May	June	July	Aug	Sept	Oct	Total
Migrant	VHF	N	75	71	66	66	50	52	75
		$\bar{x}$ locations	6.4	6.6	5.8	5.4	3.2	3.2	26.9
				Total N Migrant VHF					2,018
	GPS	N[1]	18	18	18	17	15	13	18
		$\bar{x}$ locations	316	306	292	294	256	273	1,489.5
				GPS N for RSF Models					28,301
Resident	VHF	N	41	42	40	39	32	34	44
		$\bar{x}$ locations	7.4	8	6.7	7.2	2.7	3.4	31.5
				Total N Resident VHF					1338
	GPS	N	8	8	8	7	7	7	8
		$\bar{x}$ locations	341.5	325	298	259	238	280	1,678.5
								Total N Resident GPS	13,430
Mean # of Locations/ individual elk/forage biomass interval (16-day period)									
Migrant	VHF	1.9	GPS	143	Resident	VHF	1.9	GPS	140

Notes: GPS locations collected or resampled to every 2 hours. VHF data were screened such that each elk had to have >10 locations each/summer, and the total number of elk does not equal sum of VHF and GPS because some individual elk (n=10) wore both VHF and GPS collars through the study.

Table 3-7. Differences in landscape and phenological covariates between migrant and resident elk summer summer ranges, 2002-2004, at the 2nd-order home-range scale.

	Migrant		Resident		Univariate ANOVA's†‡		
	Mean	StDev	Mean	StDev	F‡	P-value	R^2
N	44		67		---	---	---
Elevation (m)	2045.6	186.19	1779.3	143.19	64.74	<0.00005	0.37
Dist. divide (km)	39	15.71	56.6	3.79	45.08	<0.00005	0.29
Aspect richness††	5.11	0.89	3.79	0.91	57.59	<0.00005	0.35
Elevation richness††	3.12	0.52	2.02	0.49	124.17	<0.00005	0.54
Aug 5 herbaceous g/m^2	16.9	5.3	27.7	7.97	31.15	<0.00005	0.23
Aug 5 shrub g/m^2	208.9	46.8	268.5	50.14	113.1	<0.00005	0.54
Growing season length‡‡	172.98	15.32	200.53	7.07	105.9	<0.00005	0.49
Start growing season ‡‡	160.45	19.32	137.22	9.53	55.4	<0.00005	0.55

Notes: Means are the average availability within the 100% summer range calculated using zonal statistics ++ in ARCGIS 9.2. Overall MANOVA for covariates indicated significant differerences between migrant and residents (see text for details).

† - Univariate ANOVA results for each covariate. P-value evaluated at an experiment-wise error rate adjusting for multiple comparisons of P=0.05/8 = 0.00625.

‡ - All F-statistics at df_1=1, df_2=109.

††- Defined as number of different aspect or 100m elevation-classes within 360m.

‡‡- Defined based on growing season parameter models (see text).

Table 3-8. Top within home-range scale RSF models, June-Sept 2002-2004. Models estimated using logistic regression, with the coefficient(s) for forage biomass selection reported holding effects of other covariates constant (see Appendix 2).

Migrants	Overall	June	July	Aug	Sept
N used, avail	18736, 36119	5514, 9791	4970, 9811	4412, 9676	3840, 9841
$r_{s\ (SE)}$	0.78, 0.01	0.87, 0.03	0.62, 0.08	0.77, 0.02	0.78, 0.01
Coefficients	β (S.E.)	β (S.E.)	β (S.E.)	β (S.E.)	β (S.E.)
Forage shrub biomass (g/m)	0.0024 (0.0001)*	-0.0031 (0.0004)*	0.0003 (0.0004)	0.006 (0.0003)*	-0.001 (0.0003)*
Herbac. biomass (g/m^2)	0.075 (0.001)*	0.133 (0.003)*	0.186 (0.01)*	0.148 (0.004)*	-0.0156 (0)*
Herbac. biomass^2	-0.0004 (0.00001)*	-0.0006* (0.00003)	-0.0008331 (0.000049)*	-0.0007 (0.00003)*	---
Herbac. peak (g/m^2) ††	90.4	103.9	111.6	100.0	---
Form of shrub selection	*Maximize*	*Minimize*	*Maximize*	*Maximize*	*Minimize*
Form of herbaceous selection	*Intermediate*	*Intermediate*	*Intermediate*	*Intermediate*	*Minimize*
Residents	Overall	June	July	Aug	Sept
K	18	18	18	18	18
N used, avail	8736, 26966	2601, 6730	2391, 6758	2072, 6650	1672, 5288
$r_{s\ (SE)}$	0.97	0.89	0.95	0.81	-0.06
Residents	Overall	June	July	Aug	Sept

Variables	β (S.E.)	β (S.E.)	β (S.E.)	β (S.E.)	β (S.E.)
Forage shrub biomass (g/m)	0.0045 (0.0004)	-0.0017 (0.0009)	0.0051 (0.001)	0.0106 (0.0009)	0.0012 (0.0006)
Herbaceous biomass (g/m^2)	0.0805 (0.0023)	0.1697 (0.0074)	0.1633 (0.0068)	0.1258 (0.0064)	-0.0116 (0.0018)
Herbaceous biomass^2	-0.0004 (0.00002)	-0.0007 (0.00005)	-0.0006 (0.00003)	-0.0005 (0.00005)	()
Biomass Peak (g/m^2) †	114.00	116.10	133.80	115.7	
Form of shrub selection	*Maximize*	*Minimize*	*Maximize*	*Maximize*	*Maximize*
Form of herbaceous selection	*Intermediate*	*Intermediate*	*Intermediate*	*Intermediate*	*Minimize*

Notes: LL- is the log-likelihood, K the number of parameters (see appendix 2), and N the number of groups in the clogit model. Note for all models the likelihood ratio test indicated significant model fit, P-values <0.0005), Shown for each season-strategy model are the k-folds spearman rank correlation model validation test (r_s) for VHF elk locations, and the coefficient for shrub and herbaceous biomass selection and its form whether maximization, minimization, or selection for intermediate (quadratic).

* - Indicates coefficient significant at P=0.05

†- Peak biomass calculated by taking the derivative of the quadratic function.

Table 3-9. The top ranked movement-scale RSF models, June-September 2002-2004. Models estimated using logistic regression, with the coefficient(s) for forage biomass selection reported holding other covariates constant (see Appendix 2).

Migrants	Overall	June	July	Aug	Sept
N-groups, N-avail	18736, 89875	5514, 26500	4970, 24225	4412, 20885	3840, 18265
L.R. $\chi^{2,\text{ P-value}}$	1698.8, <0.0005	309.9, <0.0005	1040.2, <0.0005	1624.8, <0.0005	126.6, <0.0005
k-folds $r_{s,\ p\text{-value}}$	0.987, <0.0005	0.984, <0.0005	0.906, 0.003	0.818, <0.004	0.263, <0.56
Biomass Selection	β (S.E.)	β (S.E.)	β (S.E.)	β (S.E.)	β (S.E.)
Forage shrub biomass (g/m^2)	0.005 (0.0002)*	0.002 (0.0003)*	0.01 (0.0004)*	0.014 (0.0004)*	-0.003 (0.0004)*
Herbaceous biomass (g/m)	-0.002 (0.0008)*	0.007 (0.002)*	-0.014 (0.002)*	-0.02 (0.002)*	0.006 (0.002)*
Form of shrub selection	*Maximize*	*Maximize*	*Maximize*	*Maximize*	*Minimize*
Form of herb. selection	*Minimize*	*Maximize*	*Minimize*	*Minimize*	*Maximize*
Residents	Overall	June	July	Aug	Sept
N-groups, N-avail	2601, 12575	2391, 11455	2072, 9605	1672, 8070	8736, 41705
L.R. $\chi^{2,\text{ P-value}}$	474.1, <0.00005	158, <0.00005	154.5, <0.00005	144.32, <0.00005	88.9, <0.00005
k-folds $r_{s,\ p\text{-value}}$	0.987,	0.947,	0.794, <0.006	0.802, <0.005	-0.333, <0.33

	<0.0005	<0.0005			
Residents	Overall	June	July	Aug	Sept
Biomass Selection	β (S.E.)	β (S.E.)	β (S.E.)	β (S.E.)	β (S.E.)
Forage shrub biomass (g/m)	0.01 (0.008)*	0.009 (0.0006)*	0.02 (0.0008)*	0.02 (0.0008)*	-0.004 (0.0006)*
Herbaceous biomass (g/m^2)	0.008 (0.003)*	0.015 (0.005)*	-0.005 (0.005)	-0.02 (0.005)*	0.04 (0.007)*
Herbaceous biomass^2	-0.00003 (0.00001)*	-0.00005 (0.00003)*	----	----	-0.0002 (0.00005)*
Herbaceous Peak (g/m^2) †	140.3	141.4	----	----	86.5
Form of shrub selection	*Maximize*	*Maximize*	*Maximize*	*Maximize*	*Minimize*
Form of herb. selection	*Intermediate*	*Intermediate*	*Minimizing*	*Minimizing*	*Intermediate*

Notes: LL- is the log-likelihood, K the number of parameters (see appendix 2), and N the number of groups in the clogit model. Shown for each season-strategy model are the likelihood ratio test (all p-values <0.0005), the k-folds spearman rank correlation model validation test (r_s) for VHF elk locations, and the coefficient for shrub and herbaceous biomass selection and its form whether maximization, minimization, or selection for intermediate (quadratic).

* - indicates coefficient significant at $P = 0.05$, †- Peak biomass calculated by taking the derivative of the quadratic function.

Table 3-10. Relative diet composition by major forage class for migrant and resident elk in the YHT elk herd, summer 2002.

Month	Status	N	Forb	SE	Graminoid	SE	Shrub	SE	% Shrub Leaf
June	Migrant	4	7.4^{a}	2.52	70.0^{a*}	10.72	22.6^{a*}	7.23	0.36
	Resident	2	7.9^{a}	0.67	85.5^{a*}	0.20	6.6^{a*}	0.08	0.46
July	Migrant	9	8.2^{a*}	1.52	70.8^{a}	3.77	21.0^{a}	2.89	0.41
	Resident	5	12.4^{a*}	0.98	72.4^{a}	4.11	15.1^{a}	4.00	0.39
August	Migrant	7	15.4^{b}	3.65	54.6^{a}	6.39	30.0^{a}	4.00	0.32
	Resident	3	12.9^{b}	1.46	59.5^{b}	3.33	27.6^{b}	3.30	0.27

Notes: Does not attempt to correct for bias against detecting forbs and shrub leaves in the diet. Letters refer to post-hoc comparisons following ANOVA within a migratory and forage class between months; e.g., resident forb % diet was significantly different between June/July and August, when forb% increased. * refers to post-hoc comparisons between migrant classes within a month and forage class; e.g., % forb in diet differed between migrants and residents in July. Experiment-wise error was set at 0.10 for post-hoc Bonferonni multiple comparisons.

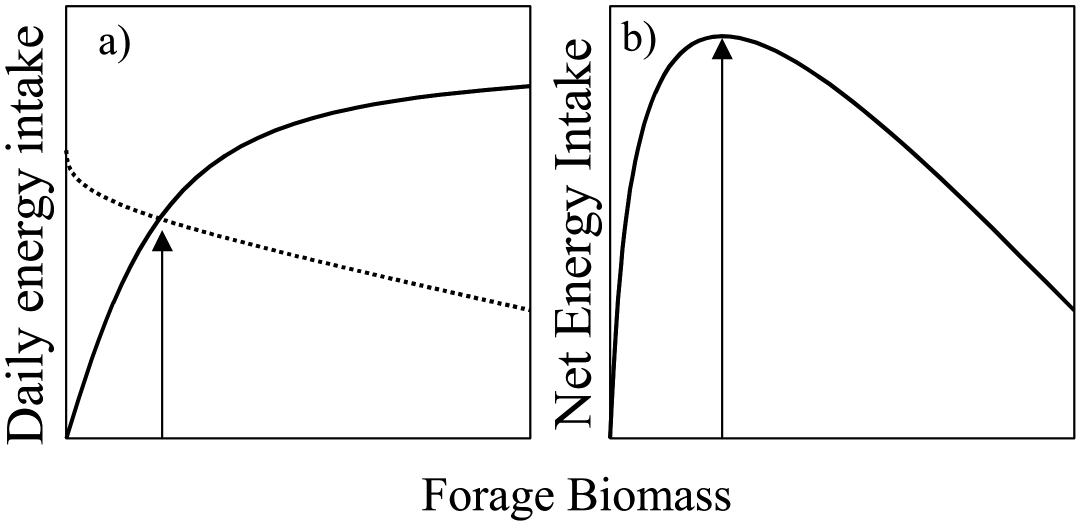
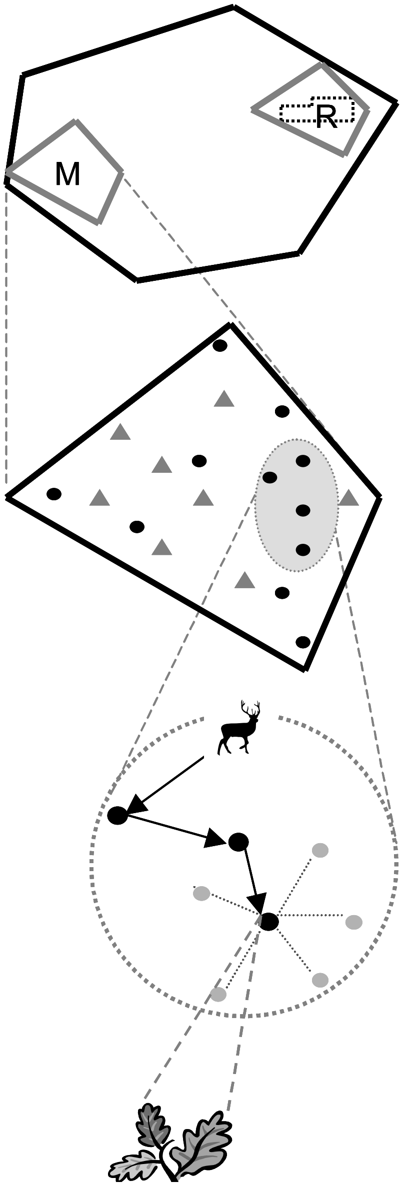


Fig. 3-1. Schematic showing general mechanisms of the forage maturation hypothesis. a) foraging constraints of cropping (solid line) and digestion (dashed line) that result in b) maximum net daily energy intake at some IFB (g/m^2). Adapted from Fryxell 1991.



Predictions of the Forage Maturation Hypothesis

a) Landscape scale between home ranges (Johnson's 2nd order)

-- Migrant elk select intermediate forage biomass (Wilmshurst et al. 1999)

- Residents select highest forage biomass by not migrating and staying at the low elevation Ya Ha Tinda ranch winter range.

b) Within home range scale (3rd order)

- Migrants relax selection for intermediate forage in home ranges because everywhere is lower within, and select maximum forage biomass (Wilmhsurst et al. 1999).

- Residents, under the FMH, would start to show selection for intermediate forage biomass to compensate for landscape scale selection.

c) Movement-path / fine-scale (3rd order)

- Migrant forage selection will continue along same trend of showing weaker selection for forage

- Residents should still show selection for intermediate forage biomass under the FMH.

d) Plant level (4th order)

- Higher dietary forage quality for migrants (Morgantini et al. 1988)

- Higher fecal nitrogen for migrants (Sakuragi et al. 2002)

Fig. 3-2. Hierarchical framework for testing forage selection under the forage maturation hypothesis at multiple spatial scales in a partially migratory elk herd, with scale specific predictions for residents and migrants.

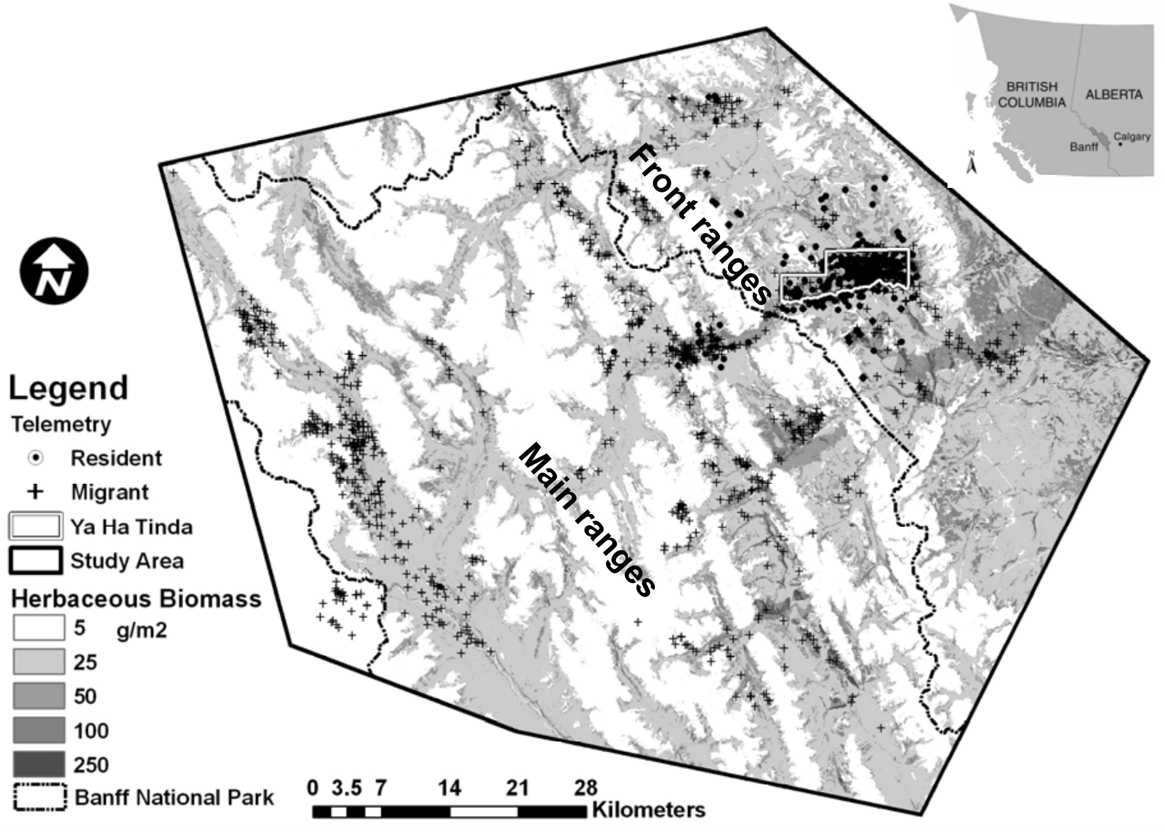


Fig. 3-3. Study area location on the eastern slopes of the continental divide in the Front and Main ranges of the Canadian Rockies, Alberta, Canada. Shown is an example of the spatially dynamic forage biomass model, the predicted total herbaceous forage biomass (g/m^2) during 2003 at the peak of the growing season (Aug 4). Resident elk (●) remain on or near the YHT Ranch during summer in the Front ranges, whilst migrants (+) migrate throughout the 6,000km^2 study area, mostly to the Main ranges, as shown by VHF telemetry data for summer 2002-2004.

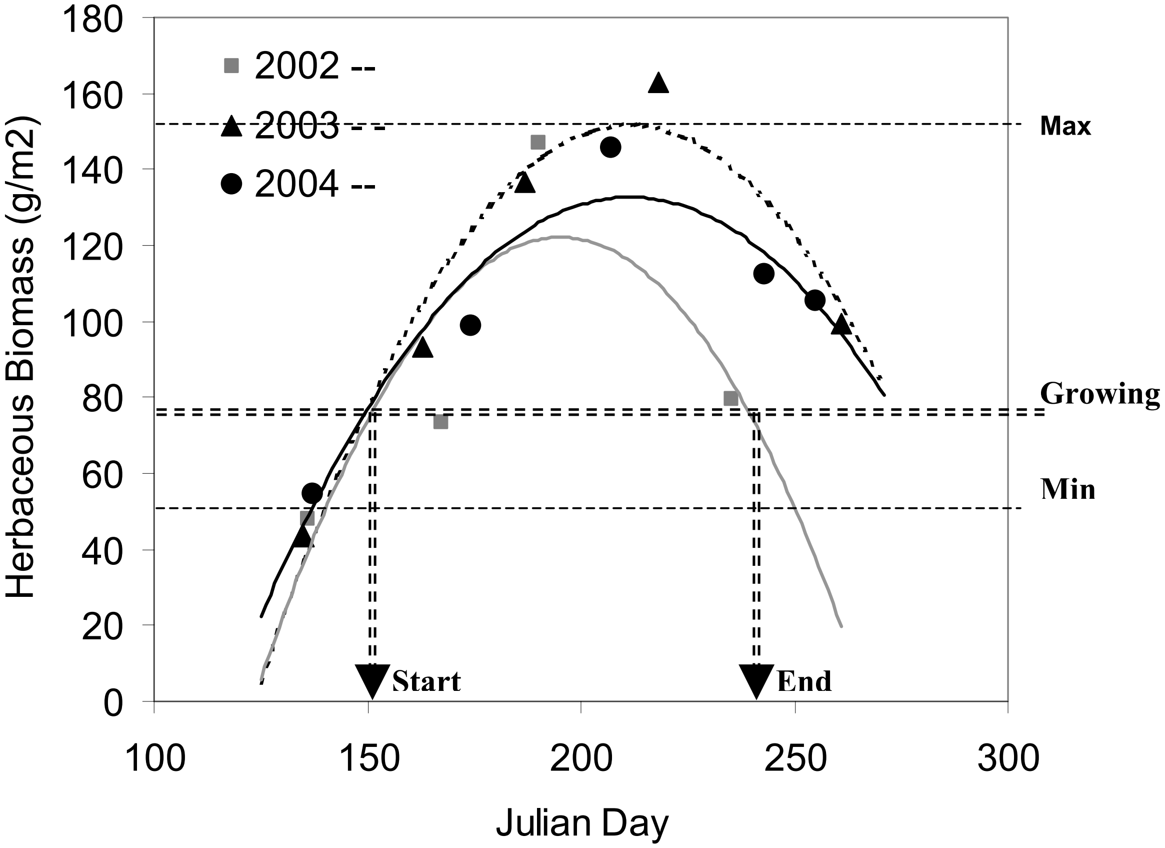


Fig. 3-4. Annual quadratic forage growth models (curved lines) for a south facing low elevation grassland site at the YHT, 2002 – 2004. The single horizontal dashed lines (---) represent the average minimum and maximum measured forage biomass for this site, and the double dashed line (= =) represents the growing threshold calculated as 25% of the difference between the min and max biomass (following Jaggoby et al. 2002). For 2002 (■) the start and end of the growing season was estimated as the intersection of the quadratic growth curve and the growing threshold, yielding start JD=151 and end of 244. See text for more details.

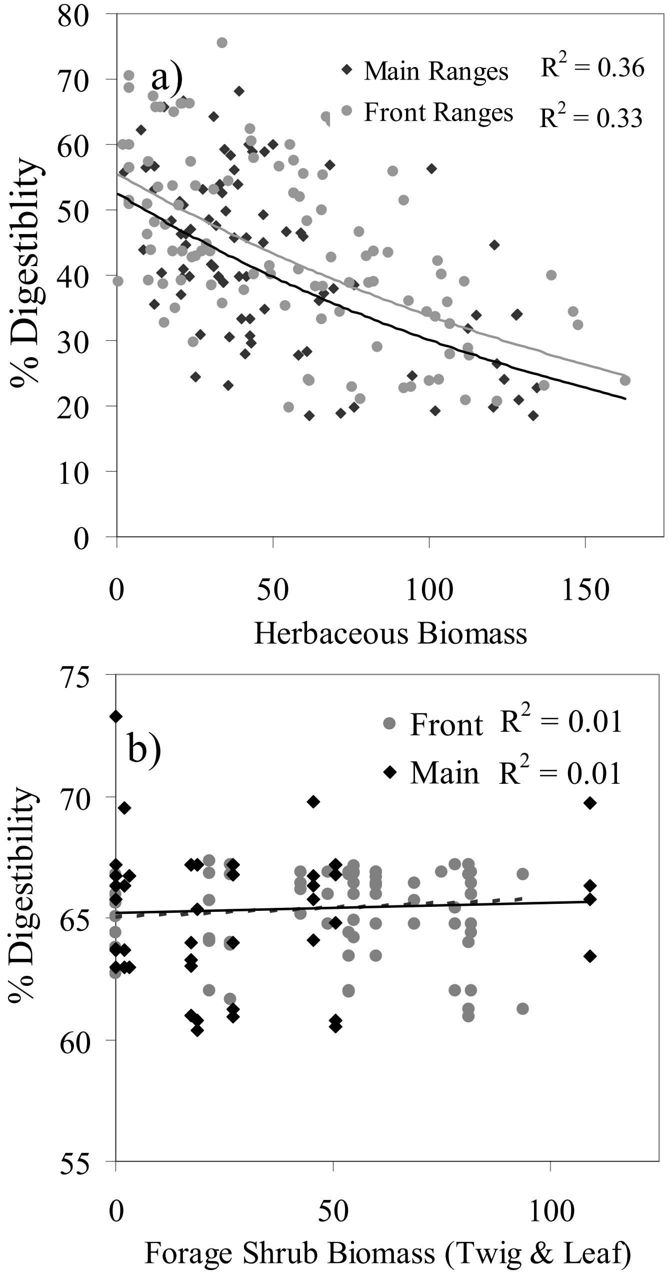


Fig. 3-5. Dry matter digestibility (%) as a function of a) herbaceous forage and b) shrub (forage spp. only) biomass from phenology plots repeat-sampled over the course of growing seasons 2002-2004. Herbaceous biomass is shown with best fit exponential decline model for the entire growing season for the Main (R^2=0.36, p<0.005) and Front ranges (R^2=0.33, p<0.005). There was no relationship between % digestibility and biomass for shrubs.

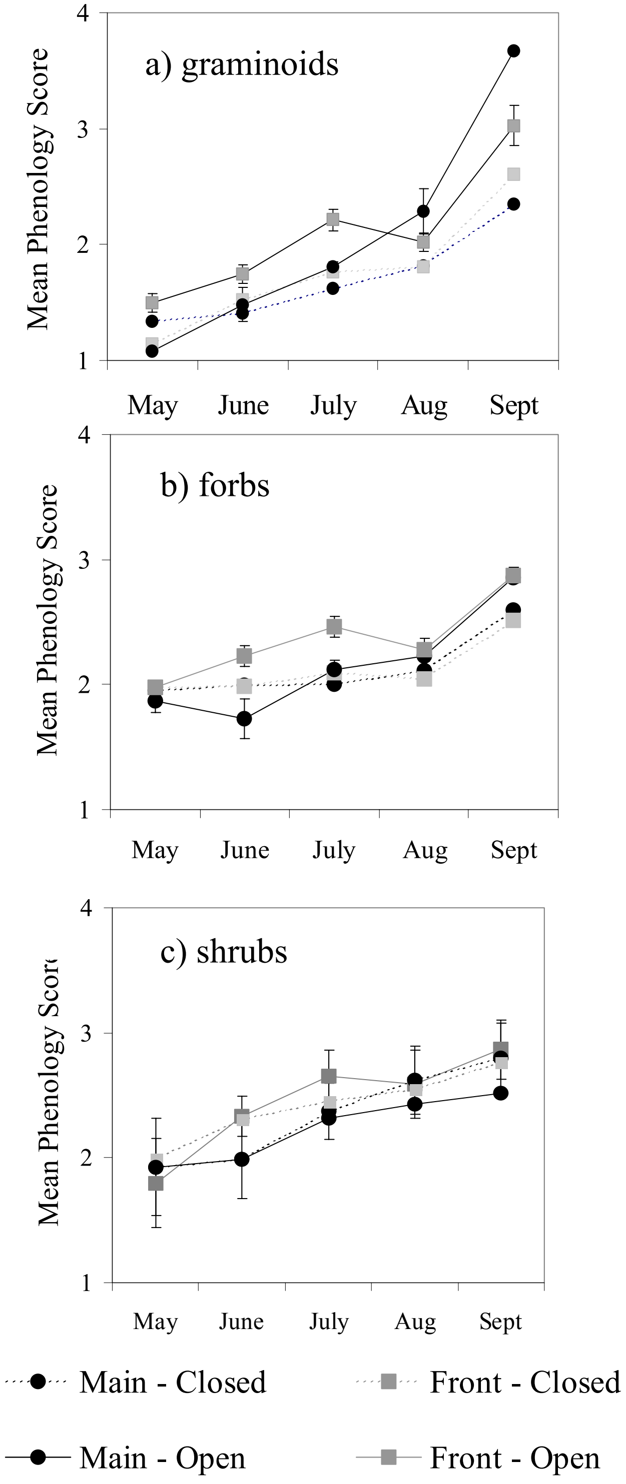


Fig. 3-6. Median a) graminoid, b) forb, and c) shrub forage species phenology scores (1-old, 2-newly emergent, 3-mature, 4-cured) in the Front (resident area) and Main (migrant area) ranges by open/closed habitat type by open/closed habitat type, eastern slopes of BNP, 2002-2004. Note SE are displayed for open habitats only for clarity.

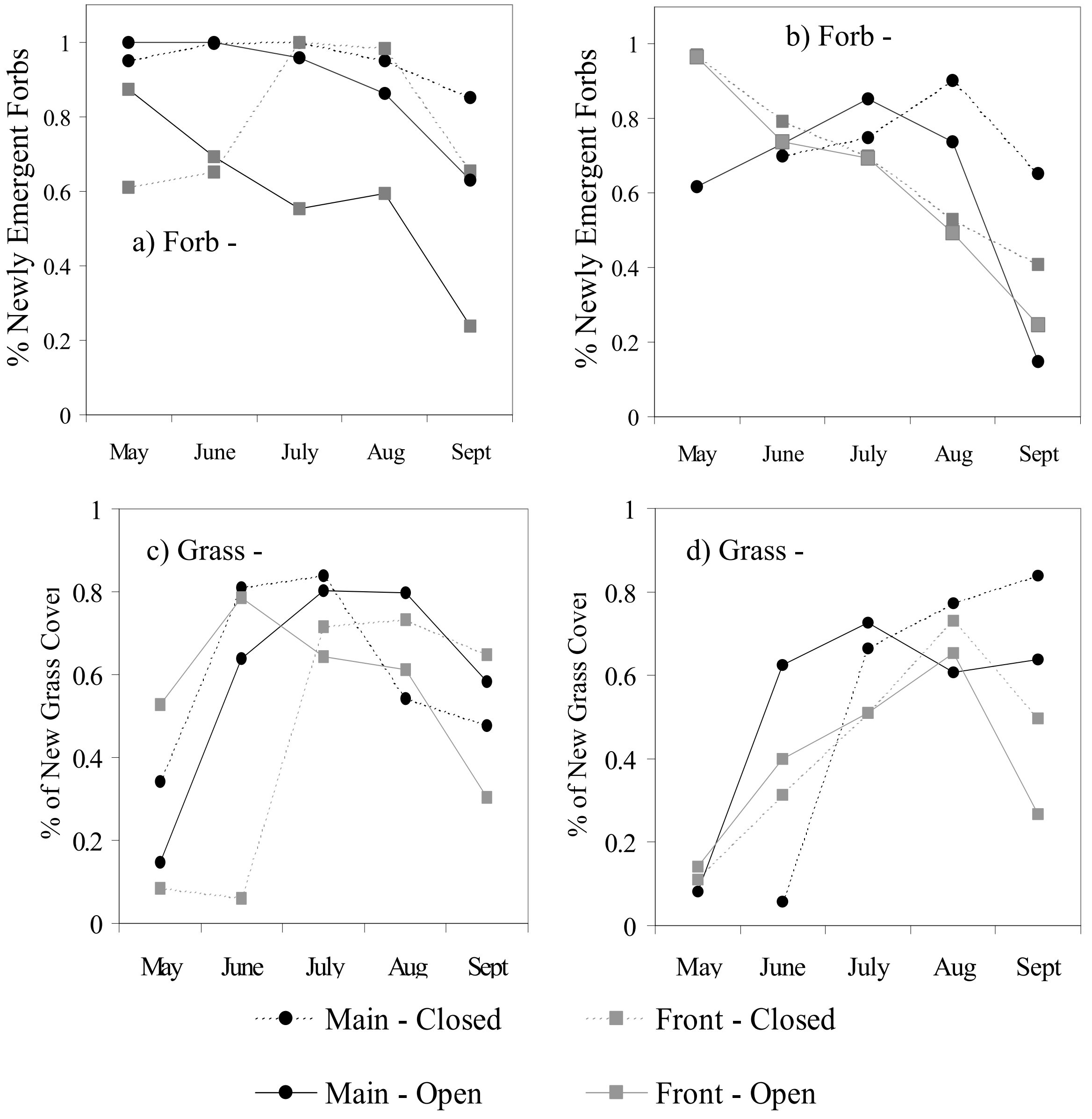


Fig. 3-7. Proportion of forage cover (biomass) in the newly emergent (highest forage quality) growth stage in the Front (resident area) and Main (migrant area) ranges for forbs at a) low and b) high elevations, and for graminoids at c) low and d) high elevations, eastern slopes of BNP, summers 2002-2004.

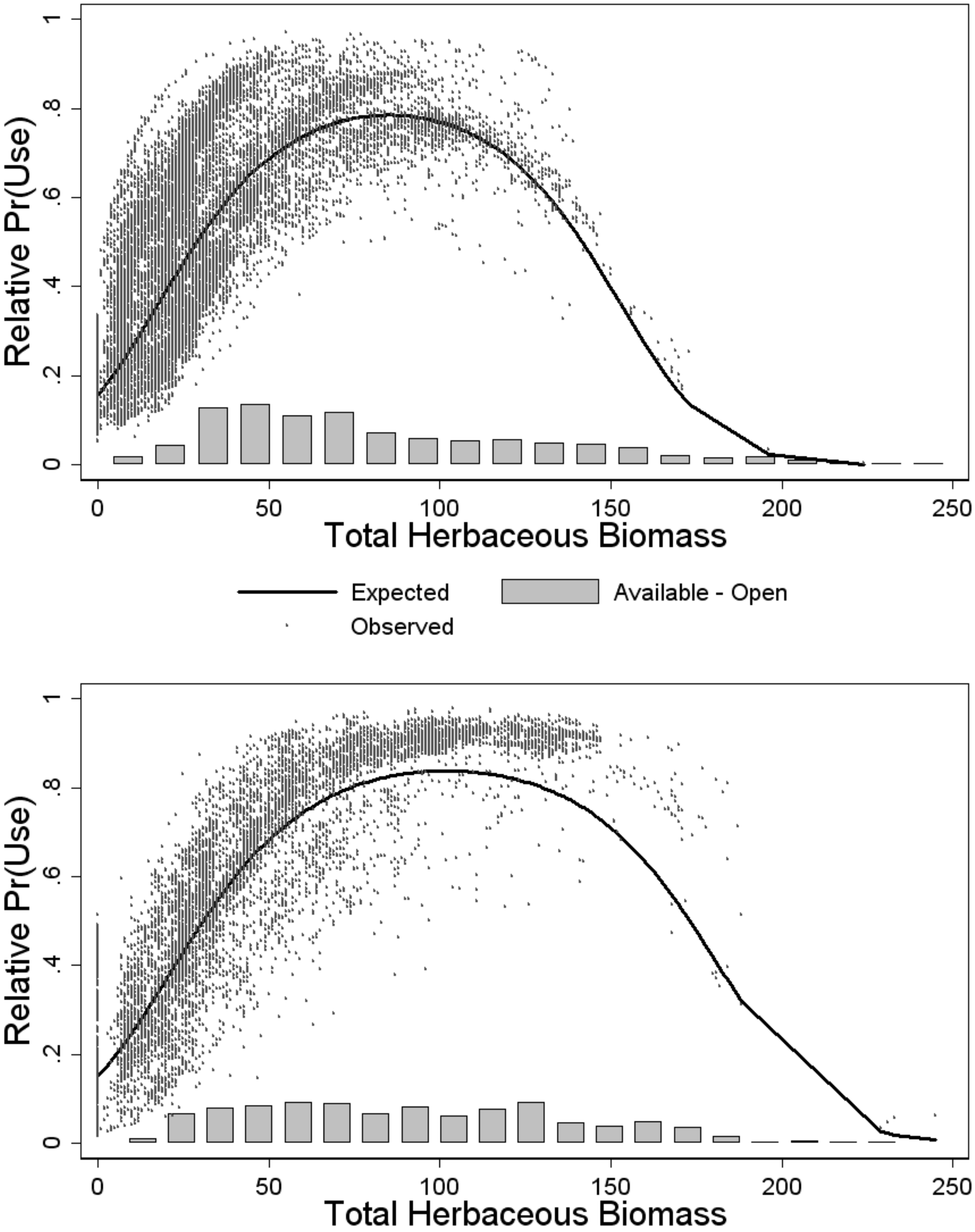


Fig. 3-8. Modeled (solid line) and observed (dots) predicted relative probability of use for GPS telemetry locations for a) migrant and b) resident elk as a function of total herbaceous forage biomass (g/m^2) in open habitats, at the home-range scale, summers 2002-2004.

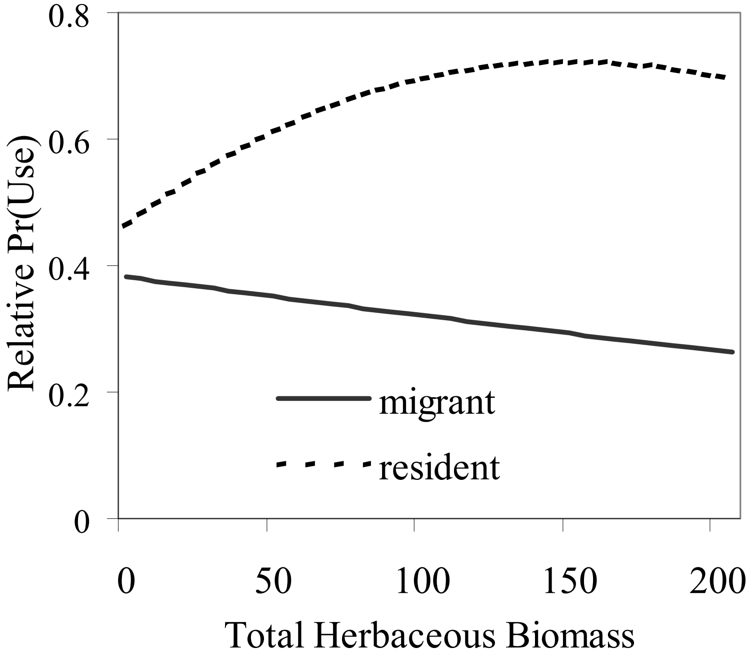
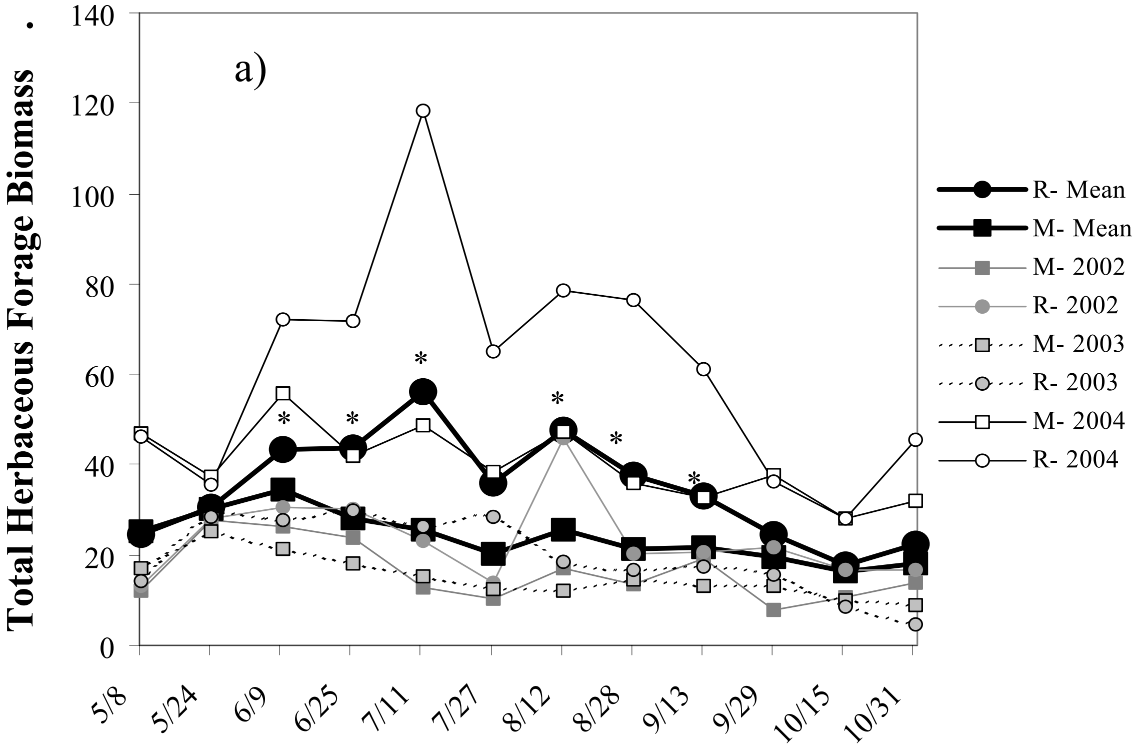
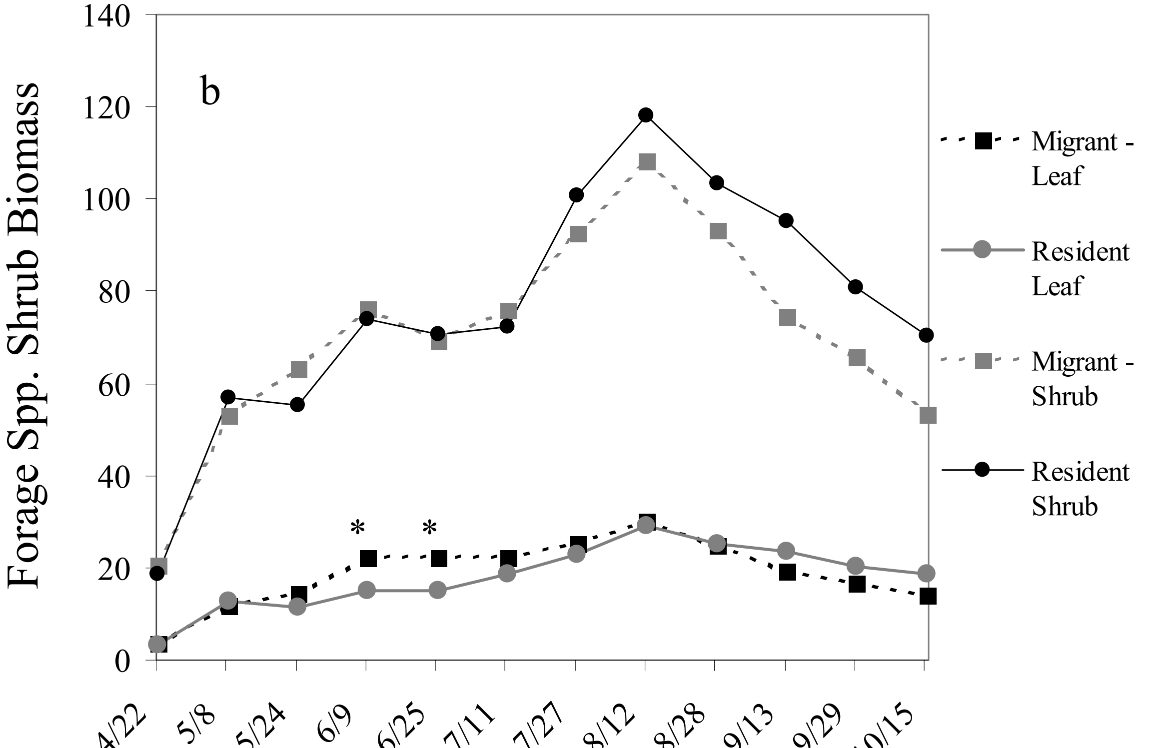


Fig. 3-9. Predicted relative probability of use for migrant and resident elk as a function of total herbaceous forage biomass (g/m^2), at movement path scale, summers 2002-2004. Evaluation of fit for clogit models was not possible in a comparable manner as Fig. 9 (Train 2004). Predictions are evaluated for a 2000m SW facing herbaceous resource unit.


a)
Total Herbaceous Forage Biomass
0
20
40
60
80
100
120
140
5/8
5/24
6/9
6/25
7/11
7/27
8/12
8/28
9/13
9/29
10/15
10/31
*
R- Mean
M- Mean
M- 2002
R- 2002
M- 2003
R- 2003
M- 2004
R- 2004


b
Forage Spp. Shrub Biomass
0
20
40
60
80
100
120
140
4/22
5/8
5/24
6/9
6/25
7/11
7/27
8/12
8/28
9/13
9/29
10/15
*
Migrant - Leaf
Resident Leaf
Migrant - Shrub
Resident Shrub

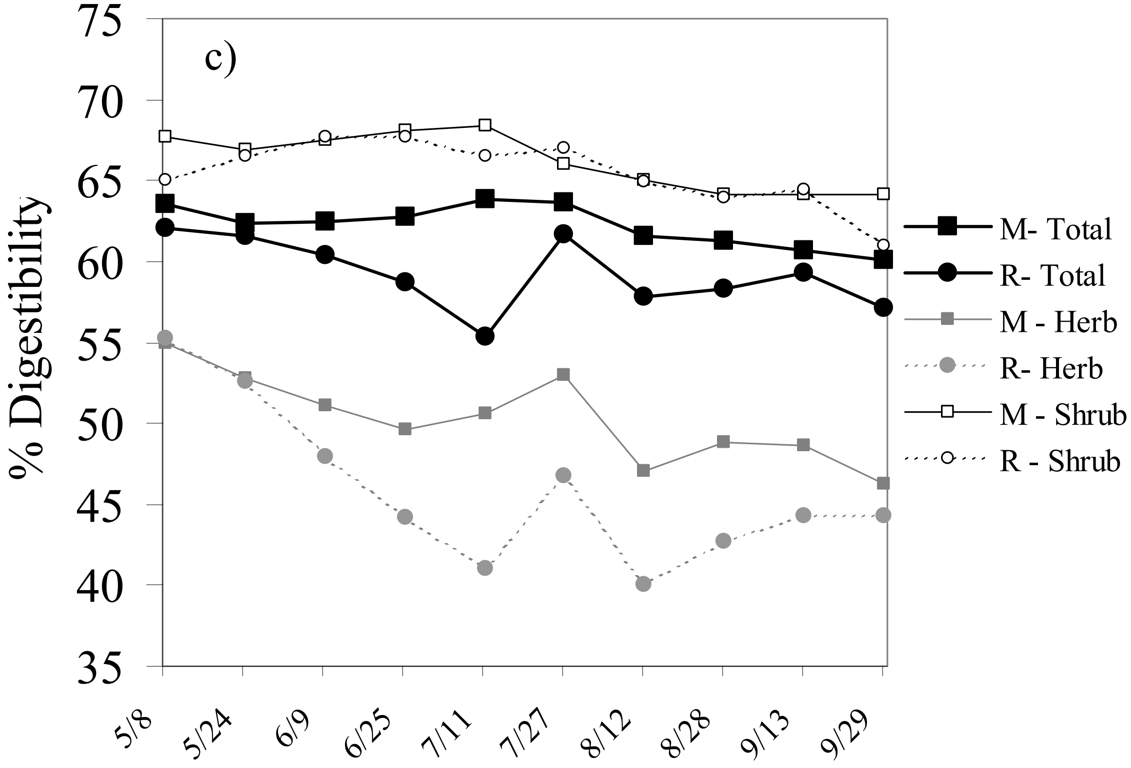


Fig. 3-10. Overall exposure of migrant (M) and resident (R) elk VHF and GPS locations to a) total herbaceous biomass (g/m^2), b) forage and leaf-forage shrub biomass (g/m^2), and c) % digestibility of herbaceous, shrub, and total forage estimated for migrant (M) and resident (R) during May to Oct, 2002-2004. Biomass values are average exposure/elk/16-day interval predicted from the random effects model with a random intercept for each individual elk. Note * indicates significant differences between migrant and resident forage biomass exposure (see text). Digestibility of herbaceous forage was calculated for average biomass values based on regressions between % digestibility and biomass from Fig. 5 and Table 1 for herbaceous. Digestibility of shrubs was calculated given average, % digestibility for each Modis interval from Table 2. See text for details.

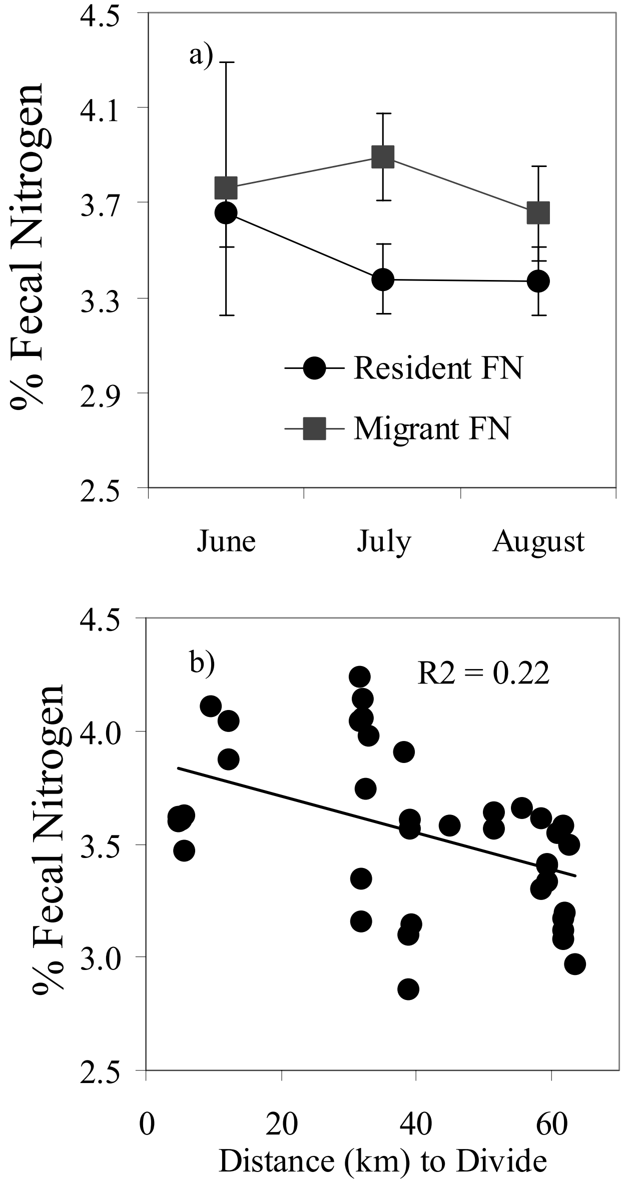


Fig. 3-11. % Fecal nitrogen in a) the diet of migrant and resident elk (with SE's), and b) as a function of distance (east) of the continental divide (with partial regression fit), eastern slopes of BNP, Alberta, Summer 2004.

LITERATURE CITED

Albon, S.D. and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos **65**:502-513.

Anderson, D.P., M.G. Turner, J.D. Forester, J. Zhu, M.S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. Journal of Wildlife Management **69**:298-310.

Baker, D.L. and N.T. Hobbs. 1982. Composition and quality of elk summer diets in Colorado. Journal of Wildlife Management **46**:694-703.

Baltagi, B.H. and P.X. Wu. 1999. Unequally spaced panel data regressions with AR(1) disturbances. Econometric Theory **15**:814-823.

Bartolome, J., J. Franch, M. Gutman, and N.G. Seligman. 1995. Factors that influence fecal analysis estimates of herbivore diets. Journal of Range Management **48**:267-270.

Bennett, O.L. and Mathias, E.L. 1984. Effects of slope and microclimate on yield and forage quality of perennial grasses and legumes. Pages 90-94 *in* H. Riley and A. O. Skjelvag editors. The impact of climate on grass production and quality. Norweigian state agricultural research station, Ås, Norway.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology **18**:320-331.

Beyer, H. 2005. Hawthtools Analysis Tools for ArcGIS. Edmonton, Alberta.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological modeling **157**:281-300.

Boyce, M. S. 1989. The Jackson Elk Herd: intensive wildlife management in North America. Cambridge University Press, Cambridge, UK.

Boyce, M.S. 1979. Seasonality and patterns of natural-selection for life histories. American Naturalist **114**:569-583.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Chen, X., Vierling, L., Rowell, E. and Defelice, T. 2004. Using Lidar and Effective Lai Data to Evaluate Ikonos and Landsat 7 Etm+ Vegetation Cover Estimates in a Ponderosa Pine Forest. Remote Sensing of Environment **91:** 14-26.

Cook, R.G. 2002. Nutrition and food. Pages 259-350 *in* D. E. Toweill and J. W. Thomas editors. North American elk: ecology and management. Smithsonian Institution Press, Washington.

Cook, J. G., Johnson, B. K., Cook, R. C., Riggs, R. A., Delcurto, T., Bryant, L. D. and Irwin, L. L. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs **155**: 1-61.

Compton, B. W., Rhymer, J. M. & McCollough, M. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): An application of paired logistic regression. Ecology, **83:** 833-843.

Craighead, J.J., G. Atwell, and B.W. O'Gara. 1972. Elk migration in and near Yellowstone National Park. Wildlife Monographs **29:** 1-49.

Dorgeloh, W.G. 2002. Calibrating a disc pasture meter to estimate above-ground standing biomass in mixed bush-veld, South Africa. African Journal of Ecology **40**:100-102.

Franklin, S.E., G.B. Stenhouse, M.J. Hansen, C.C. Popplewell, J.A. Dechka, and D.R. Peddle. 2001. An integrated decision tree approach to mapping landcover using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. Canadian Journal of Remote Sensing **27**:579-592.

Fryxell, J. M., Greever, J. and Sinclair, A. R. E. 1988. Why are migratory ungulates so abundant? The American Naturalist **131:** 781-798.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist **138:** 478-498.

Fryxell, J. M., Wilmshurst, J. F. & Sinclair, A. R. E. 2004. Predictive models of movement by

Serengeti grazers. Ecology **85,** 2429-2435.

Griffith, B., Douglas, D. C., Walsh, N. E., Young, D. D., McCabe, T. R., Russell, D. E., White, R. G., Cameron, R. D., and Whitten, R. 2002. The porcupine caribou herd. Douglas, D. C., Reynolds, P. E., and Rhode, E. B. Arctic refuge coastal plain terrestrial wildlife research summaries. Washington, USA, US Geological Survey, Biological Resources Division. Biological Sciences

Gross, J.E., L.A. Shipley, N.T. Hobbs, D.E. Spalinger, and B.A. Wunder. 1993. Functional-response of herbivores in food-concentrated patches - tests of a mechanistic model. Ecology **74**: 778-791.

Guthery, F. S., Lusk, J. J. & Peterson, M. J. 2001. The fall of the null hypothesis: liabilities and opportunities. Journal of Wildlife Management **65:** 379-384.

Hanley, T.A., C.T. Robbins, A.E. Hagerman, and C. McArthur. 1992. Predicting digestible protein and digestible dry-matter in tannin-containing forages consumed by ruminants. Ecology **73**:537-541.

Hanley, T., Cates, R. G., Van Horne, B. & McKendrick, J. D. 1987. Forest stand-age related differences in apparent nutritional quality of forage for deer in southern Alaska. Proceedings of the Symposium on plant-herbivore interactions, eds F. D. Provenza, J. T. Flinders & E. D. McArthur, pp. 9-17. US For.Ser. Gen. Tech. Report. INT-222.

Happe, P.J., K.J. Jenkins, E.E. Starkey, and S.H. Sharrow. 1990. Nutritional quality and tannin astringency of browse in clear-cuts and old-growth forests. Journal of Wildlife Management **54**:557-566.

Hebblewhite, M., E.H. Merrill, and T.E. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk system. Oikos **111:** 101-111.

Hebblewhite, M., P.C. Paquet, D.H. Pletscher, R.B. Lessard, and C.J. Callaghan. 2004. Development and application of a ratio-estimator to estimate wolf killing rates and variance in a multiple prey system. Wildlife Society Bulletin **31**:933-946.

Hobbs, N.T., D.L. Baker, J.E. Ellis, and D.M. Swift. 1981. Composition and quality of elk winter diets in Colorado. Journal of Wildlife Management **45**:156-171.

Hobbs, N.T., D.L. Baker, and R.B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. Journal of Wildlife Management **47**:1-16.

Holland, W.D. and G.M. Coen. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 1. Summary. Alberta Institute of Pedology, Edmonton.

Holroyd, G.L. and K.J. Van Tighem. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 3. The wildlife inventory. Canadian Wildlife Service, Edmonton.

Hosmer, D.W. and S. Lemeshow. 2000. Applied Logistic Regression. John Wiley and Sons, New York.

Johnson, C.J., S.E. Nielsen, E.H. Merrill, T.L. McDonald, and M.S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivations and evaluations. Journal of Wildlife Management, *In Press*.

Johnson, C. J., Parker, K. L., Heard, D. C. & Gillingham, M. P. 2002. A multi-scale behavioural approach to understanding the movements of woodland caribou. Ecological Applications, **12:** 1840-1860.

Johnson, D. H. 1980. The comparison of usage and availability measures for evaluating resource preference. Ecology **61:** 65-71.

Jorgenson, J. C., Udevitz, M. S., and Felix, N. A. 2002. Forage quantity and quality: the porcupine caribou herd. Douglas, D. C., Reynolds, P. E., and Rhode, E. B. Arctic refuge coastal plain terrestrial wildlife research summaries. Washington, USA, US Geological Survey, Biological Resources Division. Biological Sciences Report.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American Naturalist **142**:59-81.

Kawamura, K., T. Akiyama, H. Yokota, M. Tsutsumi, T. Yasuda, O. Watanabe, G. Wang, and S. Wang. 2005. Monitoring of forage conditions with MODIS imagery in the Xilingol steppe, Inner Mongolia. International Journal of Remote Sensing **26**:1423-1436.

Keating, K.A. and S. Cherry. 2004. Use and Interpretation of Logistic Regression in Habitat Selection Studies. Journal of Wildlife Management **68**:774-789.

Kikvidze, Z., F.I. Pugnaire, R.W. Brooker, P. Choler, C.J. Lortie, R. Michalet, and R.M. Callaway. 2005. Linking patterns and processes in alpine plant communities: a global study. Ecology **86**: 1395-1400.

Kudo, G., U. Nordenhall, and U. Molau. 1999. Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: comparisons along a snowmelt gradient in northern Sweden. Ecoscience **6**:439-450.

Larter, N.C. and J.A. Nagy. 2001. Seasonal and annual variability in the quality of important forage plants on Banks Island, Canadian high arctic. Applied Vegetation Science **4**:115-128.

Long, J.S. and J. Freese. 2004. Regression models for categorical dependent variables using STATA. STATA Press, STATA Corporation, College Station, TX.

Luckman, B. and T. Kavanagh. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. Ambio **29**:371-380.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Second Edition. Kluwer, Boston, USA.

McCullough, P. and J.A. Nelder. 1989. Generalized linear models. Second edition. Chapman and Hall, London, UK.

McDermid, G. J. 2005. Remote sensing for large-area, multi-jurisdictional habitat mapping. Dissertation. University of Calgary.

McNaughton, S.J. 1985. Ecology of a grazing ecosystem - the Serengeti. Ecological Monographs

55: 259-294.

McWilliam, E.L., T.N. Barry, N. Lopez-Villalobos, P.N. Cameron, and P.D. Kemp. 2005. Effects of willow (*Salix*) supplementation for 31 and 63 d on the reproductive performance of ewes grazing low quality drought pasture during mating. Animal Feed Science and Technology **119**: 87-106.

Merrill, E.H. and R.J. Anderson. 1995. Elk (*Cervus-elaphus roosevelti*) dietary-composition and quality in the mount St. Helens blast zone. Northwest Science **69**: 9-18.

Morgantini, L.E. and R.J. Hudson. 1988. Migratory patterns of the wapiti, *Cervus elaphus*, in Banff National Park, Alberta. Canadian Field Naturalist **102**: 12-19.

Morgantini, L.E. and R.J. Hudson. 1989. Nutritional significance of wapiti (*Cervus elaphus*) migrations to alpine ranges in western Alberta, Canada. Arctic and alpine research **21**:288-295.

Munro, R., M. Hebblewhite, and E.H. Merrill. 2006. Effects of post-fire logging on elk habitat during the first 3-years post burn. Forest Ecology and Management. *In prep.*

Mutanga, O., H.T. Prins, A.K. Skidmore, S. van Wiernen, H. Huizing, R. Grant, M. Peel, and H. Biggs. 2004. Explaining grass-nutrient patterns in a savannah rangeland of southern Africa. Journal of Biogeography **31**:819-829.

Mysterud, A., Langvatn, R., Yoccoz, N., and Stenseth, N. 2002. Large-scale habitat variability, delayed density effects and red deer populations in Norway. Journal of Animal Ecology **71**: 569-580.

Oosenbrug, S.M. and J.B. Theberge. 1980. Altitudinal movements and summer habitat preferences of woodland caribou in the Kluane ranges, Yukon-territory. Arctic **33**:59-72.

Pendergast, J. F., Gange, S. J., Newton, M. A. L., M.J., Palta, M. & Fisher, M. R. 1996. A survey of methods of analyzing clustered binary response data. International statistics review **64:** 89-118.

Pettorelli, N., Weladji, R. B., Holand, O., Mysterud, A., Breie, H. and Stenseth, N C. 2005a. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. Biology letters **1:** 24-26.

Pettorelli, N., Mysterud, A., Yoccoz, N. G., Langvatn, R. and Stenseth, N.C. 2005b. Importance of climatological downscaling and plant phenology for red deer in heterogenous environments. Proceedings of the Royal Society B, **272:** 2357-2364.

Pfefferman, D. 1993 The role of sampling weights when modeling survey data. International Statistical Review **61:** 317-337.

Post, E. and D.R. Klein. 1999. Caribou calf production and seasonal range quality during a population decline. Journal of Wildlife Management **63**:335-345.

Post, E. & Stenseth, N. C. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology **80:** 1322-1339.

Robbins, C.T., T.A. Hanley, A.E. Hagerman, O. Hjeljord, D.L. Baker, C.C. Schwartz, and W.W. Mautz. 1987a. Role of tannins in defending plants against ruminants - reduction in protein availability. Ecology **68**:98-107.

Robbins, C.T., S. Mole, A.E. Hagerman, and T.A. Hanley. 1987b. Role of tannins in defending plants against ruminants - reduction in dry matter digestion. Ecology **68**:1606-1615.

Sachro, L. 2002. The effects of fire on elk habitat suitability in the central Eastern Slopes of Alberta. University of Calgary. Calgary, AB.

Sakuragi, M. Igota H., Uno, H., Kaji, K., Kaneko, M., Akamatsu, R., and Maekawa, K. 2004. Benefit of migration in a female Sika deer population in eastern Hokkaido, Japan. Ecological Research **18**: 347-354.

Scott, D., J.R. Malcolm, and C. Lemieux. 2002. Climate change and modelled biome representation in Canada's national park system: implications for system planning and park mandates. Global Ecology and Biogeography **11**:475-484.

Seagle, S.W. and S.J. McNaughton. 1992. Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. Landscape Ecology **7**:229-241.

Skrondal, A. and S. Rabe-Hesketh. 2004. Generalized latent variable modeling: multilevel, longitudinal, and structural equation models. Chapman and Hall, New York, NY, USA.

Spalinger, D.E. and N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores - new models of functional-response. American Naturalist **140**:325-348.

StataCorp. 2003. Stata Statistical Software 8.0. Stata Corporation, College Station, TX, USA.

Swingland, I.R. and P.J. Greenwood. 1983. The ecology of animal movement. Oxford University Press, London.

Thoma, D. P., Bailey, D. W., Long, D. S., Nielsen, G. A., Henry, M. P., Breneman, M. C. & Montagne, C. 2002. Short-term monitoring of rangeland forage conditions with AVHRR imagery. Journal of Range Management **55:** 383-389.

Thompson, S.K. 1992. Sampling. John Wiley and Sons, New York.

Trenberth, K.E. and J.W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics **9**:303-319.

Tucker, C. J. and P.J. Sellers. 1986. Satellite remote sensing for primary production. International Journal of Remote Sensing **7:**1395-1416.

Van Soest, P.J. 1982. Nutritional ecology of the ruminant. O and B books, Corvallis, Oregon.

Vaughan, I.P. and S.J. Ormerod. 2005. The continuing challenges of testing species distribution models. Journal of Applied Ecology **42**: 730-740.

Walker, D.A., J.C. Halfpenny, M.D. Walker, and C.A. Wessman. 1993. Long-term studies of snow-vegetation interactions. Bioscience **43**:287-301.

Walsh, N.E., T.R. McCabe, J.M. Welker, and A.N. Parsons. 1997. Experimental manipulations of snow-depth: effects of nutrient content of caribou forage. Global Change Biology **3**:158-164.

White, C.A., I.R. Pengelly, M P. Rogeau, and D. Zell. 2003. Landscape fire regimes and vegetation restoration in Banff National Park, Alberta. Parks Canada, Banff, Alberta. PArks Canada Occasional Paper BNP-2003-01

White, R.G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos **40**:377-384.

Wilmshurst, J. F., Fryxell. J. M., Farm, B. P., Sinclair, A. R. E. & Henschel, C. P. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology **77:** 1223-1232.

Wilmshurst, J. F., Fryxell, J. M. & Hudson, R. J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). Behavioural Ecology **6:** 209-217.

Wilmshurst, J. F., Fryxell, J. M. & Colucci, P. E. 1999 What constrains daily intake in Thomsons Gazelles? Ecology **80,** 2338-2347.

Woods, J.G. 1991. Ecology of a partially migratory elk population. University of British Columbia.

Zar, J. H. 1995. Biostatistical analysis. Prentice Hall, London, UK.

CHAPTER FOUR

HUMAN INFLUENCES ON SPATIAL WOLF PREDATION RISK FOR ELK

INTRODUCTION

Behavioural strategies to reduce predation risk permeate ungulate life history (Conradt et al. 1999, Kjellander et al. 2004) and are often scale dependent (Rettie and Messier 2000). Perhaps the most basic anti-predator strategy is to avoid areas with high predator densities (Caro 2005), which can be achieved at several scales. For example, migratory ungulates often 'escape' predation at large spatial scales by migrating beyond the range of non-migratory predators (Fryxell et al. 1988, Seip 1992). However, in the evolutionary arms race of predator-prey dynamics (Mitchell and Lima 2002), predators can overcome large-scale antipredator strategies of prey by commuting long-distances, for example, as exhibited by Serengeti hyenas (*Crocuta crocuta*) following migratory wildebeest (*Conochaetes taurinus*) (Trinkel et al. 2004). Where large-scale avoidance is not possible, ungulates have developed behavioural strategies to reduce predation risk at finer spatio-temporal scales. Following wolf recovery in Yellowstone National Park (YNP), elk reduced use of aspen stands, a highly preferred, yet risky, foraging habitat (Fortin et al. 2005). In Banff National Park (BNP), elk avoided riskier pine and conifer stands relative to safer grasslands where the probability of being killed was lower (Hebblewhite et al. 2005a). Wolf territoriality itself provides spatial areas between territories of lower wolf predation risk that are used more by deer (Taylor and Pekins

1986, Lewis and Murray 1993). Spatial avoidance may also be time-dependent. For example, Beyer et al. (2006) showed that elk avoidance of wolves in YNP occured at night when wolves were most active. In many of these examples, ungulates avoided areas with higher wolf activity as the main mechanism of risk reduction.

Because predators themselves are subject to human-caused mortality, human activities directly and indirectly influence predator distributions and hence predation risk (Frid and Dill 2002, Beale and Monaghan 2004). Human-caused mortality, if severe enough, can obviously reduce predation risk through direct reduction of predators, such as in wolf controls (Hayes et al. 2003). In exploited populations, wolves and other predators quickly learn to avoid human activity to reduce their own predation risk by altering their spatial or temporal activity patterns (Mech and Boitani 2003). Thus, behavioural avoidance of humans by wolves may be as important as direct effects in shaping predation risk (e.g., Schmitz et al. 1997). For example, wolves avoided roads outside of Denali National in Alaska (Thurber et al. 1994), human developments in Banff (Hebblewhite et al. 2005b) and Finland (Kaartinen et al. 2005), and spatio-temporally avoided human roads and infrastructure during the day in Poland (Theuerkauf et al. 2003). In eastern Africa, both lions (Ogutu et al. 2005) and hyena's (Boydston et al. 2003) shifted away from human settlements despite higher prey densities there. These studies revealed the importance of indirect effects by humans, as well as direct effects, on fine-scale predator distribution through predator avoidance of human activity.

Recent approaches have begun to spatially model predation risk from predator distributions using resource selection functions (RSF) (Boyce and McDonald 1999) as a function of both environmental and human factors (Kristan and Boarman 2003, Frair et al. 2005, Hebblewhite et al. 2005a, Kauffman *In Review*). The simplest approaches use RSFs to model predator habitat selection as a function of availability (e.g., Johnson et al. 2002, Frair et al. 2005), assuming predator habitat use is proportional to risk (Johnson et al. 2002). An extension of this approach decomposes risk into encounter and kill components (Hebblewhite et al. 2005a), but requires data on locations of encounters and kills between predator and prey. These RSF approaches capture where predation risk occurs, but not how much, which is linked to spatial predator density (Kristan and Boarman 2003). Predation risk is a function of both the spatial density of use and the number of predators (Schmitz et al. 1997, Hebblewhite et al. 2005a). For example, Kristan and Boarman (2003) illustrated the spatial density of raven use influenced predation risk for tortoises in addition to the risk measured by a raven RSF model. In their raven-tortoise system, raven density, and hence risk, was elevated near human settlements, regardless of other habitat features. The spatial density component of risk is also expected to be especially important for territorial species where densities vary in response to social factors (e.g., Fretwell 1972, Lewis and Murray 1993, Kauffman et al. *In Review*). In a spatial context, total risk combines fine-scale risk associated with landscape attributes, and spatial predator density, or the amount of risk; for example, areas with similar landscape attributes, but vastly different spatial wolf density (Hebblewhite et al. 2005a).

To date, all approaches to spatially estimate predation risk using RSF models assumed resource selection by predators was constant across a gradient of availabilities (Mysterud and Ims 1998). Mysterud and Ims (1998) proposed animals can display variable responses in resource selection over a gradient of availability (i.e by only avoiding a risky habitat when it becomes abundant), which they termed ‘functional responses’. In the context of predator-prey dynamics, however, functional responses are usually defined as the relationship between predator kill-rate and prey density (Messier 1994, see next paragraph). Here, a functional response refers to a variable resource selelection strategy whereby selection changes across a range of availability. Regardless, few studies have modeled such functional responses in resource selection (Gillies et al. 2006). Recent advances in application of random effects models (Skrondal and Rabe-Hesketh 2004) to resource selection studies (Gillies et al. 2006) provide an approach to estimate individual or group-level variation in predation risk as a function of availability. Mixed-effects models are commonly used in the medical literature (Breslow and Clayton 1993, Begg and Parides 2003), but are underutilized in ecology (Bennington and Thayne 1994) and RSF models (Gillies et al. 2006).

In this paper I address wolf-human interactions within the range of a partially migratory elk population near Banff National Park (BNP), Canada. I test the hypothesis that predation risk for elk is shaped by wolf avoidance of humans that follows a functional response in resource selection (Mysterud and Ims 1998), where wolves show increasing spatio-temporal avoidance of humans at higher levels of human activity (Mech and Boitani 2003, Theuerkauf et al. 2003). To test this hypothesis, I first develop a novel approach to model the functional response by wolves to human activity using mixed-effects in RSF models (Gillies et al. 2006). Because wolves exhibit dramatic day/night differences in responses to human activity (Theuerkauf et al. 2003), I built separate RSF models for day/night. Next, I modeled the spatial density of use by wolves using kernel density estimators, and weight kernels by wolf pack size. I combine the wolf RSF models with spatial density of use to model the total predation risk for elk. I validate the different components of predation risk (RSF, spatial density, total) with locations of wolf-killed elk. Finally, I test the consequences of wolf avoidance of human activity for predation risk experienced by a partially migratory elk herd. In this system, 50% of elk are resident and do not migrate, remaining near the high human activity winter range year round (Chapter 2). While migration is hypothesized to reduce risk (Seip 1992), I compared multi-scale risk for migratory and resident elk to test whether wolf avoidance of human activity reduced risk experienced by resident elk.

STUDY AREA

The study area is located on the eastern slopes of the Canadian Rockies Ecosystem (CRE, White et al. 1995) in Banff National Park (BNP, 51’30’’ / 115’30’’) and adjacent provincial lands in Alberta. The study occurred between 15 Apr 2002 and 15 Oct 2004, and was defined by the movements of radio-collared wolves and elk during the study over a 7,000 km^2 area. Wolves and elk were the system’s dominant large mammalian predator and prey species. Elk are partially migratory in this system with migrants moving to summer ranges 25-50 km distant and residents residing on the Ya Ha Tinda (YHT) ranch winter range year round. See Chapter 2 for more details on elk. Other predators include grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Felis concolour*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*). Secondary ungulates include white-tailed deer, moose, mule deer (*O. hemionas*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and a remnant herd of 5-8 mountain caribou (*Rangifer tarandus*). Human activity was concentrated in the Bow Valley (BV) and YHT ranch portions of the study area where resident elk live during summer. Human use levels were the highest in the Lake Louise portion of the study area, next in the YHT, and lowest in backcountry areas (Jevons 2001). More details on vegetation, climate, and ecology of the study area can be found in Chapter 2, Holland and Coen (1983) and Holroyd and Van Tighem (1983).

Wolves recolonized the study area during the early 1980's (Paquet et al. 1996) and numbers have been remarkably stable since the late 1990's (Chapter 2, Appendix 3). Previously, Callaghan (2002) documented higher human-caused hunting and trapping mortality for wolves straddling or outside of BNP boundaries than those within BNP. During this study, 73% of radiocollared wolf mortality was by trapping and 27% was hunting related, confirming the importance of human mortality to wolves (unpublished data). On provincial lands, wolves are legally harvested ~9 months of the year, and illegally during the other three months. In comparison, human hunting on female elk was limited during the study to the fall, and legal harvest ended Fall 2003, though 26% of female elk mortality was human-caused (Chapter 6).

METHODS

I first estimated resource selection by wolves using mixed effects RSF models (Manly et al. 2002, Gillies et al. 2006) allowing pack and individual-level variation in wolves' response to human activity. I modeled the numeric component of risk by estimating the seasonal spatial density of wolves use using kernel density estimators, weighted by annual wolf pack size. Wolf RSF models and spatial density of wolves were combined to derive total risk. I then validated predation risk models with wolf-killed elk locations. Finally, I compared resident and migrant elk to test whether wolf avoidance of human activity reduced risk for resident elk in this system.

Wolf Telemetry Data

I estimated predation risk for five wolf packs overlapping the entire annual range of the Ya Ha Tinda (YHT) elk herd: the Bow Valley (BV), Cascade (CA), Ranch (RA), Red Deer (RD), and Wildhorse (WH) packs. Wolves were captured and radiocollared using modified foot-hold traps during summer, and via helicopter netgunning and limited aerial darting during winter (U. of Alberta Animal care protocol ID# 353112). I outfitted wolves with either VHF or GPS radiocollars (LMRT-3 or GPS3300sw, LOTEK Ltd.) weighing <600g. VHF collared wolves were relocated aerially or on the ground 0.5 to 1/week from a Cessna Skymaster 337. Mean VHF location error was 218m (n=20 blind trials). GPS collar data were resampled to a 2-hour relocation to keep autocorrelation structure consistent. Using the Bessel function to model GPS collar location error, 50% of all locations were <34m, and 95% were <113m (Appendix 3). I ignored these effects on habitat analyses because I found habitat-induced GPS-bias was <10% (Appendix 3, see also Frair et al. 2005). I defined two wolf-based seasons: summer (15 April-14 October) and winter (15 October to 14 April). I designated locations as day or night based on averaged monthly sunrise and sunset tables (from the Herzberg Institute of Astrophysics, NRC, http://www.hia-iha.nrc-cnrc.gc.ca/). Annual variation in daylight ranged from 7.9 to 16.6 hours.

Wolf Resource Selection Component of Predation Risk

Previous wolf resource selection (e.g., Mladenoff et al. 1995) and predation risk models (Hebblewhite et al. 2005a) ignored the hierarchical nature and non-independence of telemetry locations (level 1) of individual wolves (level 2), which are clustered within packs (level 3). Therefore, I incorporated mixed-effects into RSF models using generalized linear mixed models (GLMM) to control for group-level heterogeneity in resource selection by including random intercepts for wolves and packs. In RSF models, random intercepts account for unbalanced sample sizes and hierarchical (wolf, pack) structures (Gillies et al 2006). Mixed-effects models (mixed because they include fixed- and random-effects) also allow group-level variation in coefficients (Skrondal and Rabe-Hesketh 2004). Random coefficients could be due to individual variation in use and/or changes in the availability of covariates (Gillies et al. 2006). I used random coefficients to test the hypothesis about the role of human activity in shaping predation risk for elk by including a random coefficient for human activity. In addition, I estimated temporal (night, day) and seasonal (summer, winter) mixed-effects RSF models to test for temporal effects.

I used the common used-availability RSF design to estimate mixed-effects models (Manly et al. 2002), comparing landscape covariates at wolf GPS locations (used) and random (available) locations with a logistic model. Availability of covariates was measured at the pack-level using one random location/km^2 of seasonal territory size, estimated from the 99th kernel territory boundary (see wolf density modeling below). Only one location/km^2 was used for sake of computational efficiency: a serious drawback of the adaptive quadrature likelihood maximization procedure used is processing time (see below, Rabe-Hesketh and Skrondal 2005). For temporal risk modeling, I calculated random dates and times for random availability points to designate points seasonally and as day or night. The same random points were used for each wolf within each pack to keep availability constant for wolves within packs. I extended the used-available RSF model to include mixed effects, where the general RSF model is:

$$\hat{w}^*(x) = \exp(\mathbf{X\beta}) \qquad (1)$$

where $\hat{w}^*(x)$ is the relative probability of use as a function of covariates x_n, and $\mathbf{X\beta}$ is the vector of the coefficients $\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_n x_n$ estimated from fixed-effects logistic regression (Manly et al. 2002). For comparison to mixed-effects models, I estimated fixed-effects RSF models using Eq.1 and call this hereafter the *naïve* logit RSF. Building on Eq.1, I include random intercepts for wolves and packs via a mixed-effects GLMM with the logit link (Skrondal and Rabe-Hesketh 2004). In addition to the random intercepts, I added a random coefficient for proximity to high human use to test my human activity hypothesis. The form for a generalized three-level mixed-effects model for location *i*, wolf *j*, and pack *k,* with a random coefficient, is:

$$\text{Logit}(y_{\text{ijk}}) = \gamma_{00} + \zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \beta_1 x_{ijk} + \zeta_{1jk}^{(wolf)} x_{ijk} + \zeta_{1k}^{(pack)} x_{ijk} + \ldots + \mathbf{X\beta} + \varepsilon_{\text{ijk}} \quad (2)$$

where γ_{00} is the fixed-effect intercept, $\zeta_{jk}^{(wolf)}$ and $\zeta_{k}^{(pack)}$ are the random variation in the intercept at the wolf and pack levels, β_{i} is 'fixed' coefficient for covariate x_{ijk}, $\zeta_{1jk}^{(wolf)} x_{ijk}$ is the random variation in the 'fixed'-effects coefficient for β_1 at the wolf level, $\zeta_{1k}^{(pack)} x_{ijk}$ is the random variation in β_1 at the pack level, and ε_{ijk} is unexplained residual variation. Notation follows Rabe-Hesketh and Skrondal (2005). Note in Eq.2 the *full* model has random coefficients for both *j* and *k*, but presently, only one random coefficient can be accommodated in statistical packages (Rabe-Hesketh and Skrondal 2005). Thus, the models I examined allow coefficient variation only in *j* or *k* (see model selection below). Mixed-effect logit models were estimated with STATA 8.0 (Stata Corporation 2003) using GLLAMM (available at www.gllamm.org, sample STATA code is in Appendix 3). I derived maximum likelihood estimates (MLE's) using adaptive quadrature (Rabe-Hesketh et al. 2005) with 12 integration points following Skrondal and Rabe-Hesketh (2004). I made the following assumptions in GLMMs: (1) correlations within wolves and packs were constant, (2) correlations between wolves and packs were constant, (3) random effects were normally distributed with a zero mean and unknown variance components, and (4) GLMMs possessed a compound symmetric variance-covariance structure (see, Breslow and Clayton 1993, Skrondal and Rabe-Hesketh 2004).

A distinct advantage of mixed-effects models is the ability to provide both *marginal* and *conditional* inferences (Breslow and Clayton 1993, Skrondal and Rabe-Hesketh 2004), which in this study corresponds to *population* and *pack-level* inferences. For population RSF models, the fixed-effects estimates from Eq.2 were used in Eq.1 akin to typical RSF models (Manly et al. 2002) following:

$$\hat{w}^*(x) = \beta_1 x_{ijk} + \beta_2 x_{ijk} + .. + \mathbf{X\beta} + \varepsilon_{\mathrm{ijk}} , \qquad (3)$$

where Eq.3 is a reduced form of Eq.2 with no random intercepts nor coefficients. Although, by convention the intercept is dropped from Eq.1 (Manly et al. 2002), inclusion of a random intercept usually changes β coefficients (Breslow and Clayton 1993). Thus, in the context of predation risk, the *population*-level RSF model corresponds to the mean wolf predation risk averaged across the wolf population.

Conditional inferences in this study could be evaluated for either the individual wolf, *j*, or pack, *k*. For this study I focused on pack-level conditional inferences, but direct readers to Appendix 3 where wolf-level inferences are presented. For *pack-level* inferences, Eq.2 is solved for a specific pack, e.g., k=1 (Skrondal and Rabe-Hesketh 2004) following:

$$\hat{w}_k * (x) = \zeta_k^{(pack)} + \beta_1 x_{ijk} + \zeta_{1k}^{(pack)} x_{ijk} + .. + X\beta + \varepsilon_{ijk} \qquad (4)$$

Note Eq.4 is a reduced form of Eq.2 for just the pack-level response. Eq.4 is then solved using conditional estimates for pack k. Mixed-effects models also allow estimation of the between and within group correlations of any model. For 3-level mixed-effects models, one can estimate: (1) within pack correlation, (2) correlation between wolves in a specific pack, and (3) correlation between locations within a pack holding the effects of wolf constant. I estimated intraclass correlations following Rabe-Hesketh and Skrondal (2005); see Appendix 3 for details.

I conducted model selection in a hierarchical fashion. First, I used AIC_c (Burnham and Anderson 1998) to identify the covariates of the top fixed-effect model with their interactions from an *a priori* candidate model list. Second, using the top fixed-effects, the top mixed-effect model structure was selected using AIC_c by adding to the top-fixed effects of a: (1) random intercept for wolf, (2) random intercept for pack, (3) random intercept for wolf and pack, (4) two random intercepts and a random coefficient for packs, and (5) as previous but with a random coefficient for wolf (*sensu* Ten Have et al. 1999). For mixed-effects models, the number of parameters K was calculated as for fixed-effects models, plus a variance term for each random intercept, and a variance and covariance term for each random coefficient (Skrondal and Rabe-Hesketh 2004).

I considered the following six GIS covariates influencing wolf predation risk as fixed-effects in wolf RSF models: landcover, elevation, slope, aspect, distance to edge, and proximity to human activity. Note that ecologically, these GIS covariates served as proxies for the distribution of the ungulate prey of wolves. In the absence of spatial prey density data, however, landscape features are almost always used to map predator distributions (e.g., Mladenoff et al. 1995). Landcover type was described from an existing landcover map for the study area derived from LANDSAT-TM (Appendix 2, Franklin et al. 2001) collapsed to nine landcover types included as dummy variables: forested (the reference category which combined closed and moderate conifers, mixed, and deciduous types), open conifer, herbaceous, shrubs, deciduous, rock/ice/snow, alpine, prescribed and natural fire, and regenerating cutblocks. Because Bergman et al. (2006) found wolves selected areas closer to 'hard' habitat edges, I defined 'hard' edges as any edge between open (herbaceous, shrubs, deciduous, rock/ice/snow, alpine, prescribed/natural fire) and closed-canopied habitats (forested, open conifer) and between river and stream edges, and calculated distance (km) to these edges. The three topographic variables of elevation (m), slope (%), and aspect-class (north, south, flat) were derived from a Digital Elevation Model (DEM). Human use on linear features influenced movements of carnivores in BNP in previous studies (Paquet et al. 1996, Duke 2001, Gibeau et al. 2002). Therefore, I used the Human Use Digital Atlas of the Central Rockies Ecosystem (Jevons 2001) to quantify human activity along linear features in the study area. Human activity was updated to 2004 to include changes from the Bighorn Access Management Plan (e.g., off-highway vehicle restrictions adjacent to BNP). I combined all linear features together for analyses. Of the ~6,000 km of linear features, 40% were trails, 25% cutlines, 14% unknown, 13% off-highway vehicle trails, 5% paved roads, 2% gravel roads, and 1% railways. The average density of linear features in the study area including roads, trails, and cutlines was 0.81 km/km^2, which varied from a maximum of >7 km/km^2 at YHT and

>12 km/km^2 near Lake Louise to backcountry areas that rarely exceed 0.81 km/km^2. I used Jevons's (2001) criteria of > or < 100 human-use events/month, or expert knowledge, such as from the Central Rockies Ecosystem Interagency Liason Group (CREILG), to classify human activity level on each linear feature as either high or low. Once classified, I calculated the proximity to high human activity in km following Duke (2001) who revealed the importance of this variable to wolf resource selection in BNP. GIS covariates were calculated from 30-m^2 resolution raster maps.

I tested for a functional response in resource selection by wolves to changing availability of high human activity using pack-specific random coefficients, $\zeta_{1k}^{(pack)}$ from Eq.4. I calculated each wolf territory's mean proximity to high human activity to describe its changing availability using Hawthtools 3.19 (Beyer 2005) zonal statistics++ tool for each wolf territory. Then, for each night/day and summer/winter model, I used a logarithmic function (e.g. Mysterud and Ims 1998) to estimate the functional relationship between the dependent variable, $\zeta_{1k}^{(pack)}$, and each territory's mean proximity to high human use, $\bar{x}_k$, the independent variable.

The final mixed-effects model for each season and time of day was used to generate the population and pack-level wolf RSF. Mapping the population RSF was straightforward using GIS covariates and Eq.3 for the top model (Manly et al. 2002). However, mapping the pack-level RSF was more difficult because of the functional response. Any functional response observed is contingent on the scale of investigation (Mysterud and Ims 1998). Therefore, I used a 16-km radius moving window analysis based on the mean seasonal wolf territory size, ~800km^2 (Appendix 3) to calculate the average home range scale proximity to high human use, $\bar{x}_k$. The logarithmic functional response between $\zeta_{1k}^{(pack)}$ and $\bar{x}_k$ was then used to create a GIS coverage making $\zeta_{1k}^{(pack)}$ spatially explicit. I then substituted this spatially explicit $\zeta_{1k}^{(pack)}$ as the coefficient for human activity into Eq.4 for each landscape cell. Where necessary, spatial predictions of relative probability were rescaled between 0 and 1 (Manly et al. 2002). All RSF modeling and mapping was conducted using ARCGis 9.2 raster calculator (ESRI Ltd. 2004).

Spatial Density Component of Predation Risk

To weight the RSF by the density of wolf use over time across a territory (e.g., Kristan and Boarman 2002), I used kernel density estimators (KDE, Worton 1989) based on both VHF and GPS data of wolves. KDE's were used to derive a spatial probability density function (PDF, sums to 1) for each wolf pack in summer and winter using Hawthtools 9.0 (Beyer 2005). I then averaged seasonal values across packs to account for areas of territorial overlap where the PDF's of each pack were additive. I only estimated one winter and summer PDF, instead of separately for each year, for several reasons. First, I wanted to minimize effects of sample size bias (e.g., Powell 2000, Hemson et al. 2005) for some pack-seasons that had low sample size (e.g., CA-winter 2002/03, n=21). Second, wolf pack spatial distributions were very stable during the study (Appendix 3). Three packs (CA, BV, WH) raised pups at the same densite and the two packs that changed dens (RD and RA) did so only for one summer out of three. Moreover, both packs made use of either the same den or rendezvous sites during all three summers (RD/RA), or had multiple litters at both den-sites (RA). Therefore, I felt it justified using one seasonal PDF for each season during the study. To minimize effects of autocorrelation and sample sizes between wolf packs on PDF (Girard et al. 2002, Hemson et al. 2005), I followed Girard et al.'s (2002) recommendation to sample one location per day at random per VHF and GPS collared wolf/pack. Recent studies illustrate the 'art' of selecting an appropriate smoothing factor, *h,* for KDE's (Hemson et al. 2005). Although Hemson et al. (2005) recommended against using least squares cross validation (LSCV) for estimating *h* with large sample sizes from GPS collars, they provided few solutions to this problem. Because my objective was to derive large-scale estimates of density of space use, I used the largest LSCV smoothing factor *h* for wolf-pack season kernels, 4250m, which was set equal for all wolf packs to ensure consistency. I used the 99% percentile of these seasonal KDE's to define wolf territory boundaries for RSF modeling above (Appendix 3).

Next, I weighted the average seasonal kernel density estimators for seasonal differences in pack size during every year of the study. Maximum pack sizes were estimated during winter and summer (including pups) from sightings, snow tracking, and den observations. Pups were included in summer to account for the extra hunting, and hence predation risk, required to feed larger litters (Mech and Boitaini 2002). Predation risk for elk is not simply a linear function of pack size, but is more likely related to the number of elk killed per unit time by a pack. To determine the *relative* increase in predation risk with pack size, I modeled the non-linear relationship between kill-rate•day^{-1}•pack^{-1} (Y) and wolf-pack size (X)(e.g., Thurber et al. 1994) using previous data from Hebblewhite et al. (2004) for the same study area. The best non-linear model between pack size and kill-rate•day^{-1}•pack^{-1} was $Y = 0.385*(1.00 - 0.726^{X})$, $r^2=0.40$, $F_{1,25}=15.85$, $P<0.0005$). Using this regression, I calculated the expected kill-rate for each pack during the five seasons of my study assuming similar kill-rates during summer. Each territory was then weighted for each season relative to the increase in kill-rate over a minimum pack size of two.

I then combined the wolf RSF model and wolf pack density to model the spatial density component. For each season I used the appropriate kernel density estimators for all five packs multiplied by the seasonal pack size weighting function to create five seasonal relative wolf density functions from summer 2002 to summer 2004.

Total Predation Risk and Model Validation

I multiplied the RSF by the spatial density to estimate the total predation risk for elk, using day and night population- and pack-level RSF models. I validated predation risk models using out-of-sample locations of wolf-killed elk. I considered these kill locations as a strong form of model validation because kill data were not used in development of the predation risk models, yet strongly reflected risk for elk (Hebblewhite et al. 2005a, Chapter 6). Values of risk components (e.g., RSF, spatial density, and total) at locations of wolf-killed elk were compared to area-adjusted frequency of the components of predation risk (similar to k-folds cross-validation, Boyce et al. 2002). I located wolf-killed elk from 1999 to 2005 through snow backtracking (e.g., Hebblewhite et al. 2004), concurrent radiocollared elk mortality studies (Chapter 6; McKenzie 2001), and summer aerial telemetry on collared wolves. Because I did not know the time of day for most kills, I used averaged predation risk during both night and day. I calculated the area-adjusted frequency of available wolf predation risk function measures in 10 deciles in the GIS and compared this to the frequency of wolf-killed elk within the same bins, following k-folds cross validation. The correspondence between the ranked RSF-availability bins and frequency of wolf-killed elk was assessed using Spearman's rank correlation (r_s). I considered values >0.90 as indicating high predictive accuracy.

Evaluating Population and Pack-Level Predation Risk for Elk

I compared elk predation risk exposure using the population and pack-level models to test the hypothesis that wolf avoidance of human activity reduced risk for elk. Mean risk exposure for VHF and GPS elk locations was calculated over four 'elk' seasons: spring (April/May), summer (June, July, August; the main migratory period), fall (September/October), and winter (November-March), for a total of 11 seasons between 2002 and 2004. Elk exposure to wolf risk was measured at both population- and pack-levels by associating elk locations with the appropriate temporal (night/day) and seasonal (summer/winter) wolf predation risk models. I then tested for differences between migrants and residents in risk exposure (Y) using linear mixed-effects models with a random-effect for each elk (Skrondal and Rabe-Hesketh 2004), autocorrelation term, and dummy variables for migratory status, seasons, and season*migrant interactions using XTREGAR in STATA 8.0 (Baltagi and Wu 1999, StataCorp 2003) following:

$$Y_{it} = \beta_0 + \beta_M X_{1i} + \beta_2 X_{2i} + \ldots + \beta_n X_{ti} + \boldsymbol{\beta_M X_t} + \gamma_i + \rho\varepsilon_{i,\,t-1} + \eta_{it} \qquad (5)$$

where Y_{it} is the predation risk for elk i=1 during season t, β_M is the average effect of migrant elk, $\beta_{2...t}$ are the seasonal coefficients (spring 2002, etc), $\boldsymbol{\beta_M X_t}$ is the vector of season*status interactions, γ_i is the random effect of elk i, $\rho\varepsilon_{i,\,t-1}$ is the first-order autocorrelation, and η_{it} is the random error. XTREGAR is robust to unbalanced observations in both i and t and seasonal gaps in t for i (Baltagi and Wu 1999). I used backwards-stepwise model selection to select the best model and compared the population and pack-level models for seasonal differences in risk between migratory strategies.

RESULTS

I captured 30 wolves from the five packs, outfitting 16 with GPS and 14 with VHF collars. Not including wolves with <15 VHF locations/season, I retained 20 wolves from which I obtained 17,575 GPS and 257 VHF locations, for an average of 541 GPS locations/season, and 28 VHF locations/wolf. I only used 15 wolves with GPS collar data from for RSF modeling. For modeling spatial density of use, I selected one location/day at random from all 30 wolves to better capture spatial distribution of all wolves for an average of 261 random locations per pack/season (Table 4-1).

Wolf Resource Selection Component of Risk

Model selection results confirmed that it is not really a question of whether to include random effects in terms of model fit, but how (Table 4-2, 3). Adding any random effect dramatically improved fit over the naïve logit by hundreds of ΔAIC units. For all seasonal and time of day models, the top model was selected with certainty, and included random intercepts for wolf and pack, and a pack-level random coefficient for proximity to high human use (model $\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(pack)} x_{1ijk}$, Table 4-2, 3). Interestingly, the model $\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(wolf)} x_{1ijk}$ failed to converge during summer, but not during winter, when it was still a distantly second-ranked model (Table 4-3). I discuss reasons for this below.

Within the top summer models, the fixed-effects influencing wolf resource selection were relatively consistent across temporal and seasonal scales, with a few exceptions. Wolves strongly avoided steeper slopes and strongly selected for areas closer to ‘hard’ edges (Table 4-4). Wolves also selected burned and alpine habitat during summer, but selected burns less and avoided alpine completely in the winter (Table 4-4). Avoidance of higher elevations was mirrored by stronger avoidance of rock during winter. Seasonal differences between selection for herbaceous and shrubs were not as different as temporal differences; wolves selected both more at night than day (Table 4-4). Finally, open conifer and cutblocks were selected during summer, but were as equally avoided as forested habitats during winter (Table 4-4). Coefficients in Table 4-4 represent the population-effects accounting for the hierarchical data structure of wolves within packs, and are not equal to the naïve-logit estimates, which I discuss shortly in comparison to the random coefficient.

During the day in summer, the correlation among wolves within packs, ρ(pack), and among wolves for a specific pack, ρ(wolf, pack), were relatively similar, 0.62 and 0.69 respectively. Wolves within packs were less correlated than with other packs at night in summer (0.15 vs. 0.55, respectively). This continued during the winter where different packs were not correlated at all during either night or day ($\rho = 0.11, 0.03$) but wolves within a specific pack were highly correlated ($\rho = 0.909,\ 0.907$). Finally, locations for an individual wolf were more correlated during the day during both seasons than at night (Table 4-4). In all cases, the correlation among wolves within a pack, ρ(wolf, pack), was always greater than between packs, > ρ(pack), as theoretically expected (Skrondal and Rabe-Hesketh 2004).

I compared the population-level coefficient for proximity to high human use in Table 4-4 to the coefficient from the naïve logit in Fig. 4-1. The naïve-logit consistently showed no selection by wolves to human activity. In contrast, pack-level wolf selectivity for proximity to high human use at the home-range scale changed dramatically between packs within seasons (Table 4-5, Fig. 4-1). The BV pack always selected areas closer to human activity. The RA pack did similarly except during daytime in the winter when they selected areas away from human activity, but the WH pack did the opposite, selecting areas far from humans except during the day in winter. Finally, both the CA and RD pack consistently selected areas far from human activity (Table 4-5, Fig. 4-1).

I found evidence that wolf selection for human activity did indeed change across availability and time of day according to a functional response relationship (Fig. 4-2, Table 4-5, 6). As human activity increased, wolves in high human activity areas became constrained within their home ranges to select areas close to human activity, whereas packs in areas with much lower human activity within their territories, such as the CA and RD packs, ignored human activity (Fig. 4-2, Table 4-6). The functional response interacted with time of day such that wolves in high human activity areas moved closer to human activity during nighttime, but spatially avoided such areas during the day. This interaction was observed for the BV, RA, and WH packs, the latter, only during winter (Fig. 4-2). The spatial effects of this functional response are illustrated using a GIS map of the top summer RSF models in Fig. 4-3. Fig. 4-3 shows a portion of the study area across a wide gradient in human activity, from the high human activity near the YHT ranch to the centre of BNP with the lowest human activity in the study area. Using the population-level model, little difference between night and day was observed (Fig. 4-

3c,d), and the population effect of wolves selecting areas close to high human use (Fig. 4-1) drove the elevated wolf predation risk near the YHT and dramatically lower risk in the RD territory (Fig. 4-3). In contrast, the pack-level RSF models illustrated the dynamic application of the functional response. Little change occured between night and day inside BNP in the RD territory, but a dramatic night/day difference in risk occurred at the YHT in areas of high human activity because of the difference in the functional response between night and day (Fig. 4-3a,b).

Spatial Density Component of Risk

Wolf use was more concentrated in a restricted area in wolf territories during winter (Fig. 4-4), focused on the YHT, and other smaller elk winter ranges within BNP such as the lower Red Deer, Panther-Dormer rivers, and lower BV areas. During summer, density shifted west and was more diffuse, yet strongly influenced by the proximity to wolf dens (Fig. 4-4). The RD pack made extensive use of the areas north of Lake Louise during summer, the RA pack expanded to the northwest, the CA pack shifted south, and the BV pack expanded west into British Columbia. Wolf pack sizes ranged from a low of 2 to a high of 21 during the study (Table 4-7), with an average of 8.6 wolves in winter and 10.9 wolves in summer. Total number of wolves ranged from 40 in 2002 to 62 in 2004. Thus, densities ranged from 5.7 – 8.9 wolves/1,000km^2, not including lone wolves. Relative (to a pack size of 2) wolf-kill rates ranged from 1 (i.e., a pack size of 2) to a maximum of 2.40 (21).

Total Predation Risk and Model Validation

Total risk was highest surrounding wolf dens in the Panther valley, Red Deer valley, near YHT, and the lower BV (Fig. 4-5). Between 1999 and 2005, I collected 197 locations of wolf-killed elk, n=67 during summer (72% of known sex-age elk were adult female), and n=134 during winter (54% were adult female). The pack-level total predation risk model predicted wolf-killed elk locations the best (r_s=0.972, P<0.0005) of the total risk, density, and RSF-only predation risk models. The population-level total predation risk model performed second best (r_s=0.910, P<0.0005), followed by the pack-level (r_s=0.895, P=0.0015), and marginal PRF model (r_s=0.881, P=0.005). Wolf density alone predicted the locations of wolf-killed elk the poorest (r_s=0.775, P=0.02). The pack-level total predation risk model for summer (average of day/night) in Fig. 4-5 shows that total wolf predation risk predicts spatial locations of wolf-killed elk (Fig. 4-5).

Evaluating Population and Pack-Level Predation Risk for Elk

From the top population-level predation risk linear mixed-effects model (XTREGAR Wald χ^2=17.85, p<0.022, R^2_{overall} = 0.20, $R^2_{\text{within-elk}}$=0.30, $r^2_{\text{between-elk}}$=0.03, $\rho\varepsilon_{i,\,t-1}$=0.49), predation risk was the same for migrant and resident elk during all time periods except for summer 2002 (β=–0.17, SE=0.08) and summer 2003 (β=–0.09, SE=0.04) when migrant risk was significantly lower than residents (Fig. 4-6). The relative magnitude of the difference between migration strategies in these two summers was 24% lower risk for migrants during summer 2002, 28% lower during summer 2003, and 12% in summer 2004, for an average 22% lower risk for migrants compared to residents during summer (Fig. 4-6). Given the pack-level predation risk model, however, benefits of migration were reduced (Wald χ^2=14.85, p<0.007, $R^2_{overall}$= 0.20, $R^2_{within\text{-}elk}$=0.30, $R^2_{between\text{-}elk}$=0.03, $\rho\varepsilon_{i,\ t\text{-}1}$=0.44). Predation risk differed only between migrant and resident elk during summer 2003 (β=−0.02, SE=0.01) Moreover, migrant risk was only 9, 28, and 8% lower during 2002-2004, respectively. On average, given pack-level risk, migrant predation risk was reduced by only 15% and only significantly so in one of three summers (Fig. 4-6). Note that population and pack-level predation risk are relative and not directly comparable. Therefore, the lower magnitude for relative pack-level risk does not infer lower risk relative to the population-level model.

DISCUSSION

Individual wolves responded to the proximity to human activity more similarly within, than between, wolf packs in mixed effects RSF models. This was because wolf packs that occurred in areas far from high human activity neither selected nor avoided to be close to human activity at any time of day. However, as human activity increased at the territory scale, wolf packs spatio-temporally avoided humans during the daytime, when human activity is the highest (e.g., Fig. 4-2). These subtle differences between wolves and packs were efficiently estimated in a mixed-effects RSF model, which allowed wolves within packs to respond similarly to human activity. Incorporating these 'mixed-effects' lead to vastly different conclusions about the consequences of wolf avoidance of humans for elk exposure to wolf predation risk. Ignoring differences in resource selection between packs using a naïve population-level wolf RSF model would have led to the conclusion that migration reduced predation risk significantly in all three summers of the study by 24%. In comparison, the pack-level wolf RSF model, which accommodated this variable response of wolf packs to human activity, revealed migrants reduced risk significantly only in one of three summers by only 15%. This indicated that wolf predation risk for elk was influenced at fine spatial scales by wolf avoidance of human activity during the daytime. These results are generally corroborated by previous studies of wolf resource selection. The fixed-effects described in wolf RSF models, namely avoidance of steep slopes, selection to be close to hard edges, and general selection for higher forage biomass habitat types as expected to match patterns of their prey are similar to previous studies of wolves (Callaghan 2002, Bergmann *In Press*, Whittington et al. 2004,). However, the mixed-effect RSF modeling approach provided a framework to understand the often-contradictory conclusions of previous studies of wolf-human interactions.

Even a cursory review of the wolf-human literature reveals these contradictions. For example, at large scales, early studies in the Great lakes region indicated wolves avoided areas with road densities above 0.6 km/km^2 (Thiel 1985, Mech et al. 1988, Wyveden et al. 2001). Exceptions to this rule, however, quickly emerged both in the Great lakes region (Merrill 2000), and in Europe where wolves frequently use high human activity areas (Mech and Boitani 2003, Theuerkauf et al. 2003). Results have also been contradictory at finer-scales within the home range. Wolves selected seismic lines in the boreal forests of Alberta (James 1999), avoided paved but selected dirt roads with low human activity in Italy (Ciucci et al. 2003), variably selected to be close or far from human activity in the Canadian Rockies dependent on human activity levels (Callaghan 2002, Whittington et al. 2004), and avoided human activity in a sparsely populated region of Finland (Kaartinen et al. 2005). Unfortuneately, the metrics typically used to measure human activity (road density, distance to roads, etc) do not capture whether human activity occurred on them or not. Whittington et al. (2004) and others (Callaghan 2002) suggested that wolves respond to more to the level of human activity on linear features rather than linear feature density per se (e.g., Forman and Alexander 1998, Frid and Dill 2002). They suggest wolves are attracted to use human linear features at low human activity, but avoid them as human activity increases (Callaghan 2002, Whittington et al. 2004). My study tested this hypothesis in a quantitative framework across a wide gradient of human activity, summarized by the functional response in Fig. 4-2. In areas of low human activity, wolves showed no selection for this variable. As human activity increased (at the scale of the wolf home range) wolves were constrained to select areas closer to human activity, and spatio-temporal segregation began to occur (Fig. 4-2). This quantitative relationship confirmed wolves respond to linear features dependent on activity levels, as suggested by Whittington et al. (2004). For example, the boreal forests of Alberta are characterized by low human activity, yet high road density, and wolves there frequently used linear features (James 1999). As human activity increases, wolf packs in the Canadian Rockies avoided human activity (Callaghan 2002, Whittington et al. 2005), consistent with Fig. 4-2. And at the highest human activity levels, wolves in Poland had no choice but to spatio-temporally avoid human activity (Theuerkauf et al. 2003). Given the evolutionary and recent history of human persecution of wolves by humans (Musiani and Paquet 2004), these responses are surely adaptive for wolves. Future studies of wolf-human interactions could improve and refine this functional response concept, and I propose it will be a useful framework to examine wildlife-human relationships across systems.

Including mixed-effects in RSF models provides a unified approach to include functional responses, and also overcome other common limitations of resource selection studies. For example, previous studies pooled across wolves and/or discarded data to estimate a fixed-effects logit across packs to reduce autocorrelation (e.g. Mladenoff et al. 1995, Kaartinen et al. 2005). Mixed-effects RSF models account for autocorrelation by appropriately treating individuals and groups as the sampling unit (Rabe-Hesketh and Skrondal 2004). They can also accommodate unbalanced sampling designs in RSF studies (Gillies et al. 2006), provide estimates of intraclass correlations, and account for hierarchical data in one unified model. As a comparison with conventional approaches, Callaghan (2002) recognized the importance of pack-level variation, but after modeling resource selection separately for each wolf pack, combined data into one population-level model. Yet, Fig. 4-1 reveals the limitations of averaging models because the population effects are not equivalent to the pack-level responses, nor are the naïve logit effects (see also Begg and Parides 2003 and Skrondal and Rabe-Hesketh 2004 for discussion). Likewise, estimating one RSF model per wolf pack and then averaging coefficients would not necessarily be equivalent to the marginal estimate, and would not allow true-population level inferences (Bennington and Thayne 1994, Begg and Parides 2003). Furthermore, mixed-effects RSFs provide estimates of the intraclass correlations between/among groups. Intraclass correlations revealed resource selection by wolves was as similar within as among packs during summer, but was less similar among packs as within packs during winter. These correlations are consistent with seasonal wolf ecology. During summer, breeding pairs are the primary caregivers to the pups, social cohesion breaks down, and younger wolves hunt in scattered groups (Mech and Boitani 2003). In winter, wolves hunt as cohesive unit (Mech and Boitani 2003). Thus, pack-specific responses to landscape covariates and/or prey selection may be the greatest during winter. These features of mixed-effects RSF models will apply to a variety of other resource selection settings, and will help overcome many of the limitations of habitat selection studies (Garshelis 2002).

Spatial measures of wolf density revealed that wolf RSF models alone would be inadequate to adequately reflect predation risk experienced by elk. Spatial wolf density was driven by proximity to wolf den sites, which were restricted to the eastern portion of the study area in low elevation valley bottoms, thereby influencing the total predation risk model (Fig. 4-5). Similarly, Kristan and Boarman (2003) showed that raven predation risk for tortoises was a function of habitat use and spatial densities. Raven habitat selection was a function of distance to roads and human settlements, yet raven densities were also influenced by distance to active nests, and both influenced risk for tortoises. With wolf predation on elk, the importance of combining spatial density with the RSF was confirmed because the total predation risk model (a product of the two) showed a stronger relationship to out-of-sample elk kill locations in model validation. Regardless of evidence from this study that 'total' predation risk was the best predictor of predation risk, the relative importance of spatial density vs. RSF patterns remains unknown. This has important implications for management questions regarding whether changing the number of predators, or their resource selection patterns, would be the 'best' approach to influence predation risk for elk. For example, in areas of high human use, would the relative gains from reducing (or increasing) human use say, by 50%, be equivalent to an increase (or decrease) of wolf density? While I examined differences in predation risk components between migrants and residents in Chapter 5, future research is needed on the links between predator-prey dynamics and spatial predation risk before these questions may be answered (Hebblewhite et al. 2005a).

Regardless of questions over the relative importance of risk components, resident elk were clearly benefiting by exploiting fine-scale predation risk refugia relative to the population-level wolf RSF models. Thus, ecologists should consider the influence of humans when determining predation risk (Frid and Dill 2000). Had I ignored the pack-level variation in responses to human activity, I would have concluded migration significantly reduced risk by 24% in all three summers, instead of weaker benefits of migration including pack-level differences. In comparison to the literature on migratory ungulates, these results were quite surpising. Bergerud et al. (1984) proposed the widely supported (e.g., Seip 1992) hypothesis that migration in mountains reduces predation risk because of the avoidance of areas of high wolf density. In my study, however, residents reduced risk by exploiting fine-scale refugia created by high human activity levels associated with increasing recreation at the YHT. Thus, further multi-scale refinements to Bergerud et al.'s (1984) generalized hypothesis may be needed. For example, predation risk may be avoided at multiple spatial scales (Rettie and Messier 2000, Dussault et al. 2005), but this remains to be tested for this wolf-elk system.

Under lower historical levels of human recreational activity, the benefits of the spatial refugia created by wolf avoidance of humans would be diminished. However, when human use levels were lower 25 years ago (Morgantini 1988), there were also far fewer wolves (Chapter 2, Morgantini 1988), and therefore a weaker gradients in predation risk to interact with human activity. As human and wolf activity increased, the refuge likely developed as elk learned to avoid wolves by associating with human activity. Similar changes to the predation risk landscape are occurring throughout western North America. Resident elk populations are increasing on agricultural lands with reduced human hunting pressure in Montana (Burcham et al. 1999), and urban elk populations near townsites are growing (Hebblewhite et al. 2005b). Thus, reducing human activity may be required to restore predator-prey dynamics, exemplified in the Bow Valley of BNP where human activity reductions appeated to increase wolf use of these areas (Duke et al. 2001, Duke 2001). Alternatively, within the context of long-term ecosystem dynamics, year-round human hunting may have the same effect (White et al. 1998), despite its management unpalatability. An intermediate solution may be required, such as aversive conditioning of elk by humans to counteract predation refugia (Kloppers et al. 2005). Because human activity is continuing to increase in western North America, further human disruption of predation risk seems likely without active management, with potential effects beyond the wolf-elk system.

Trophic consequences of wolf avoidance of human activity seem likely based on results of research from other systems (e.g., Schmitz et al. 1997, White et al. 1998, Hebblewhite et al. 2005b). Resident elk that avoided predation risk by selecting areas closer to human activity appeared to enjoy increased survival rates, leading to higher densities (Chapter 6). Higher resident elk density has important implications for overgrazing and conservation of both rough fescue (*Festuca campestris*) (McInenly 2003) and aspen communities (White et al. 2003). Because conservation concern for fescue overgrazing is highest in summer, when wolf avoidance of high human activity would be also be the greatest, increasing elk densities as a result of wolf avoidance of humans may cascade down to grassland dynamics. The growing appreciation of indirect effects on trophic relationships (e.g., Schmitz et al.1997, Fortin et al. 2005) suggests the importance of predator avoidance by elk for overgrazing fescue and aspen communities at the YHT.

My results firmly demonstrate that random effects are really a property of the experimental design (Bennington and Thayne 1994, Rabe-Hesketh and Skrondal 2004) and not necessarily something to be arrived at using a model selection framework. Bennington and Thayne (1994) made a strong plea for ecologists to admit much of the sampling done in ecology should be analyzed in a random-effects framework. For example, without random effects, researchers can really make only valid inferences to the sampled units, not the population (Breslow and Clayton 1993, Bennington and Thayne 1994, Skrondal and Rabe-Hesketh 2004). Certainly, in some situations random effects may be useless for some resource selection situations, where, for example, animals illustrate constant or highly conserved selection patterns. Regardless, it seems likely that in many cases, random effects should be considered *a priori* as inherent aspects of experimental design for resource selection studies. Doing so will undoutedly open new avenues of research, for example, individual-level inferences from mixed-effects models may provide a crucial link between resource selection and fitness (Cam et al. 2002). As a preliminary example, the RA pack wolf (#77) that selected areas the closest to human activity (Appendix 3) was subsequently shot by a hunter. This suggests a tantalizing fitness consequence of this individual resource selection strategy. Furthermore, partitioning individual-inferences by age- and sex-class may also provide insight into potential life-history consequences of resource selection strategies. In my study, breeding female wolves demonstrated the most 'conservative' human avoidance behaviour of age-sex classes in Appendix 3. Future studies will undoubtedly harness the ability of mixed-effects models to measure individual-level variation in resource selection.

In summary, I provided an empirical example of mixed-effects RSF models in the literature for a continuous covariate that illustrates Mysterud and Ims (1998) functional response in habitat selection concept. The few previous studies that did examine such functional responses usually compared resource selection among separate areas (Osko et al. 2004), and only rarely developed continuous selection responses (Mysterud and Ims 1998, Mauritzen et al. 2003). The flexibility of a mixed-effects approach efficiently captured the changing selection of wolves to the availability of human activity levels within their home ranges. I illustrated that the consequences of contrasting inferences from the population and pack-level can have dramatic biological relevance for predation risk for elk, for example. I found support for the hypothesis that wolf avoidance of human activity reduced predation risk for resident elk, thereby equalizing benefits of migration between strategies during summer. Thus, future studies of predation risk for ungulates may benefit from considering humans as key participants in the predator-prey dynamic. These findings have important implications for the demographic consequences of migration in this population. While migration is expected to reduce predation risk, I showed that in some circumstances, residents were capable of exploiting fine-scale refugia to mitigate costs of not migrating. However, some of the reduction in risk I observed with residents at the pack-level may have been a result of fine-scale trade-offs between risk and forage, which I tested for in Chapter 5. While migrants benefited from migration due to forage (Chapter 3) and reduced predation risk in one summer, the increasing resident elk population in this study area (Chapter 2) suggests interactive effects between forage and predation risk may be additionally benefiting resident elk.

Table 4-1. Seasonal wolf pack data used for kernel density estimation and predation risk analysis, 2002-2004.

Pack	Season	KHR Sample size†	99% KHR	No. collared wolves	No. GPS collared wolves	No. used points‡	HR-scale No. random points††
Bow Valley- BV	Summer	216	786.9	3	2	1838	750
Bow Valley- BV	Winter	99	459.3	1	3	1908	906
Cascade- CA	Summer	194	730.7	2	1	1273	395
Cascade- CA	Winter	283	604.3	3	1	623	302
Red Deer- RD	Summer	612	1035.9	6	4	3998	2940
Red Deer- RD	Winter	129	1471.7	4	3	2412	635
Ranch- RA	Summer	551	750.6	6	3	3916	1125
Ranch- RA	Winter	249	523.3	6	3	1390	825
Wildhorse- WH	Summer	170	622.1	2	1	1496	311
Wildhorse- WH	Winter	107	830.6	3	2	810	833

† - Sample size of locations from 1/day/wolf used for Kernel estimation.

‡ - Total number of wolf locations (VHF and GPS) used in PRF model.

†† - Number of random points used to characterize availability within the seasonal 99% kernel home range.

Table 4-2. Summer-day and night fixed and random effects RSF model selection table for wolves in the eastern slopes of BNP, 2002-2004, showing model structure, number of fixed and random parameters, LL, n, AIC, and ΔAIC.

Model Name and Structure	# Fixed k	# Random k	k	LL	n	AIC	ΔAIC
Daytime model							
$\mathbf{X}\beta$	11	0	11	-4518.4	10,294	9058.8	861.8
$\zeta_{jk}^{(wolf)}$	11	1	12	-4181.3	10,294	8386.6	189.6
$\zeta_{k}^{(pack)}$	11	1	12	-4405.2	10,294	8834.4	637.4
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)}$	11	2	13	-4181.3	10,294	8388.5	191.5
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(wolf)} x_{1ijk}$	*Failed to converge†*			---	---	---	---
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(pack)} x_{1ijk}$	11	4	15	-4083.5	10,294	8196.9	0.00
Night model							
$\mathbf{X}\beta$	11	0	11	-3456.1	7,544	6934.2	628.5
$\zeta_{jk}^{(wolf)}$	11	1	12	-3251.4	7,544	6526.8	221.1
$\zeta_{k}^{(pack)}$	11	1	12	-3440.8	7,544	6905.7	600.0
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)}$	11	2	13	-3252.0	7,544	6529.9	224.2
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(wolf)} x_{1ijk}$	*Failed to converge†*			---	---	---	---
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(pack)} x_{1ijk}$	11	4	15	-3137.9	7544	6305.7	0.00

Notes: model structures are **X**β **-** fixed effects naïve logit model, $\zeta_{jk}^{(wolf)}$ - random intercept for effect of wolf, $\zeta_{k}^{(pack)}$ - random intercept for pack, $\zeta_{1jk}^{(wolf)} x_{1ijk}$ - random coefficient for distance to high human use for individual wolves, $\zeta_{1jk}^{(pack)} x_{1ijk}$ - random coefficient for proximity to high human use for wolf packs.

†- Convergence failure is thought to have occurred because, for the same second-ranked winter model (Table 4), ρ(wolf, pack) < ρ(pack) (unpubl.data), a biologically nonsensical result (Skrondal and Rabe-Hesketh 2004).

Table 4-3. Winter-day and night RSF fixed and random effects RSF model selection table for wolves in the eastern slopes of BNP, 2002-2004, showing model structure, number of fixed and random parameters, LL, n, AIC, and ΔAIC.

Model Name and Structure	# Fixed k	# Random k	k	LL	n	AIC	ΔAIC
Daytime model							
Xβ	9	0	9	-2727.6	4776	5473.1	1178.9
$\zeta_{jk}^{(wolf)}$	9	1	10	-2205.1	4776	4430.1	135.9
$\zeta_{k}^{(pack)}$	9	1	10	-2442.8	4776	4905.6	611.4
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)}$	9	2	11	-2158.9	4776	4339.7	45.5
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(wolf)} x_{1ijk}$	9	4	13	-2143.2	4776	4312.4	18.2
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(pack)} x_{1ijk}$	9	4	13	-2134.1	4776	4294.2	0
Night model							
Xβ	9	0	9	-2647.9	5268	5313.8	1184.5
$\zeta_{jk}^{(wolf)}$	9	1	10	-2125.1	5268	4270.2	140.9
$\zeta_{k}^{(pack)}$	9	1	10	-2354.7	5268	4729.3	600.1
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)}$	9	2	11	-2060.3	5268	4142.5	13.3
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(wolf)} x_{1ijk}$	9	4	13	-2053.5	5268	4133.0	3.7
$\zeta_{jk}^{(wolf)} + \zeta_{k}^{(pack)} + \zeta_{1jk}^{(pack)} x_{1ijk}$	9	4	13	-2051.6	5268	4129.3	0

Notes: model structures are **Xβ -** fixed effects naïve logit model, $\zeta_{jk}^{(wolf)}$ - random intercept for effect of wolf, $\zeta_{k}^{(pack)}$ - random intercept for pack, $\zeta_{1jk}^{(wolf)} x_{1ijk}$ - random coefficient for distance to high human use for individual wolves, $\zeta_{1jk}^{(pack)} x_{1ijk}$ - random coefficient for proximity to high human use for wolf packs.

Table 4-4. Structure of the top seasonal (summer, winter) and temporal (night, day) 3-level mixed-effects RSF models with random intercepts for wolf and pack levels, and a random coefficient at the pack-level for wolf response to proximity to high human use.

	Summer RSF Model				Winter RSF Model			
	Day Model		Night Model		Day Model		Night Model	
N - level1	10294		7544		4776		5268	
N - level 2	11		11		13		13	
N- level 3	5		5		5		5	
Condition No.	171.5		111.7		139.6		118.3	
Fixed effects	*Day*	*SE-Day*	*Night*	*SE-Night*	*Day*	*SE-Day*	*Night*	*SE-Night*
Intercept	1.92	0.066*	1.54	0.283*	0.77	0.377*	1.14	0.402
Dist. To High Human use	-0.15	0.014*	-0.12	0.064	-0.22	0.128	-0.21	0.109
Distance to Edge (km)	-1.31	0.120*	-1.52	0.147*	-1.23	0.187*	-1.38	0.204
Slope	-0.08	0.003*	-0.09	0.004*	-0.07	0.005*	-0.11	0.005
Burn	1.37	0.113*	1.13	0.131*	0.24	0.146	0.32	0.142
Alpine	0.53	0.114*	0.13	0.129	-0.48	0.23*	-0.65	0.237
Shrub	0.99	0.131*	1.15	0.140*	0.11	0.147	0.93	0.159
Rock	-0.46	0.089*	-0.46	0.105*	-1.43	0.152*	-0.95	0.171
Open conifer	0.52	0.100*	0.38	0.102*				
Herbaceous	0.54	0.161*	1.40	0.170*	0.72	0.189*	1.29	0.161
Cutblock	0.59	0.285*	1.36	0.390*				
Random effects	Variances and Covariances							
$\zeta_{jk}^{(wolf)}$	0.238	0.023	0.930	0.344	9.200	3.370	9.870	3.660
$\zeta_{k}^{(pack)}$	2.083	0.177	0.343	0.013	1.260	0.603	0.331	0.375
$\zeta_{1jk}^{(pack)} x_{1ijk}$	0.269	0.039	0.085	0.031	0.459	0.296	0.200	0.173
	Summer RSF Model				Winter RSF Model			
	Day Model		Night Model		Day Model		Night Model	
Fixed effects	*Day*	*SE-Day*	*Night*	*SE-Night*	*Day*	*SE-Day*	*Night*	*SE-Night*
COV(Pack-Wolf)	0.268	0.041	-0.107	0.058	-0.069	0.072	-0.111	0.086
COR(Pack-Wolf)	0.358	---	-0.622	---	-0.091		-0.433	
Intraclass correlations								

ρ(pack)	0.618	0.148	0.109	0.029
ρ (wolf, pack)	0.689	0.549	0.909	0.907
ρ (pack |wolf)	0.665	0.247	0.546	0.240

Notes: variances, e.g., $\zeta_{jk}^{(wolf)}$ are same as in Table 3. * indicates significant at P=0.05.

†- Condition number is an index of how well the model is identified. In binomial models, where model identifiably is difficult, values less than a few hundred are not cause for overt concern (Rabe-Hesketh and Skrondal 2005). See appendix 3.

†† - This is the covariance between the random intercept and random coefficient at the pack level.

‡ - This is the correlation between the random intercept and random coefficient at the pack level.

‡‡- Intraclass correlations measure the correlation between wolves within the same pack (ρ(pack)), within an individual wolf in a specific pack k (ρ(wolf, pack)), and between locations for a given individual wolf, holding the effects of different packs constant (ρ(pack |wolf)).

Table 4-5. Conditional estimates of random intercepts $\zeta_{k}^{(pack)}$ and coefficients $\zeta_{1jk}^{(pack)} x_{1ijk}$ and their standard errors (SE) at the pack-level from the top 3-level mixed effects RSF model for wolves on the eastern slopes of BNP, 2002-2004.

Wolf Pack	Bow Valley		Cascade		Ranch		Red Deer		Wildhorse	
Summer - Day Models										
$\zeta_{k}^{(pack)}$	2.63	(0.471)	1.830	(0.355)	2.95	(0.284)	0.73	(0.252)	2.26	(0.474)
$\zeta_{1jk}^{(pack)} x_{1ijk}$	-0.40	(0.072)	0.007	(0.020)	-0.35	(0.029)	0.10	(0.010)	0.25	(0.052)
Summer – Night										
$\zeta_{k}^{(pack)}$	2.16	(0.429)	1.340	(0.384)	2.03	(0.358)	0.99	(0.336)	1.20	(0.421)
$\zeta_{1jk}^{(pack)} x_{1ijk}$	-0.66	(0.097)	0.033	(0.021)	-0.50	(0.039)	0.08	(0.012)	0.24	(0.056)
Winter – Day										
$\zeta_{k}^{(pack)}$	1.17	(0.549)	0.997	(0.622)	0.92	(0.455)	0.42	(0.094)	0.19	(0.988)
$\zeta_{1jk}^{(pack)} x_{1ijk}$	-0.91	(0.289)	0.083	(0.024)	0.03	(0.061)	0.08	(0.019)	-0.12	(0.072)
Winter Night										
$\zeta_{k}^{(pack)}$	1.55	(0.526)	1.11	(0.495)	1.14	(0.500)	0.95	(0.499)	0.84	(0.508)
$\zeta_{1jk}^{(pack)} x_{1ijk}$	-1.56	(0.225)	0.05	(0.024)	-0.17	(0.059)	0.04	(0.021)	0.06	(0.068)

Notes: inferences at the wolf-level are possible given this model using $\zeta_{jk}^{(wolf)}$, but are not reported for brevity.

Table 4-6. Wolf –human use functional response model parameter estimates between the selectivity coefficient (Y) and seasonal wolf home range-scale proximity to high human use (X). Non-linear model form $Y = \beta_0 + \beta_1 * \text{Ln}(X)$

Model	β_1	SE	β_0	SE	$F_{1,4}$	P	R^2-Adj
Summer - Day	0.2	0.085*	-0.232	0.107*	5.62	0.095	0.54
Summer - Night	0.291	0.097*	-0.356	0.17*	8.84	0.058	0.66
Winter - Day	0.295	0.13*	-0.3562	0.17	4.77	0.110	0.45
Winter - Night	0.49	0.19*	-0.722	0.245*	6.33	0.085	0.57

Notes: Model estimated using non-linear least squares, and * indicates significant at a conservative P=0.10 because of small sample size.

Table 4-7. Wolf pack sizes (including pups) during summer (s) and winter (w) seasons 2002-2004, eastern slopes of BNP.

Pack Size	s02	w0203	s03	w0304	s04
Bow Valley- BV	4	2	3	2	5
Cascade- CA	11	9	9	7	13
Red Deer- RD	14	12	16	14	16
Ranch- RA	14	11	17	17	18
Wildhorse-WH	7	6	7	6	10
Total	50	40	52	46	62

Notes: s02 refers to summer 2002, w0203, winter 2002-2003, etc.

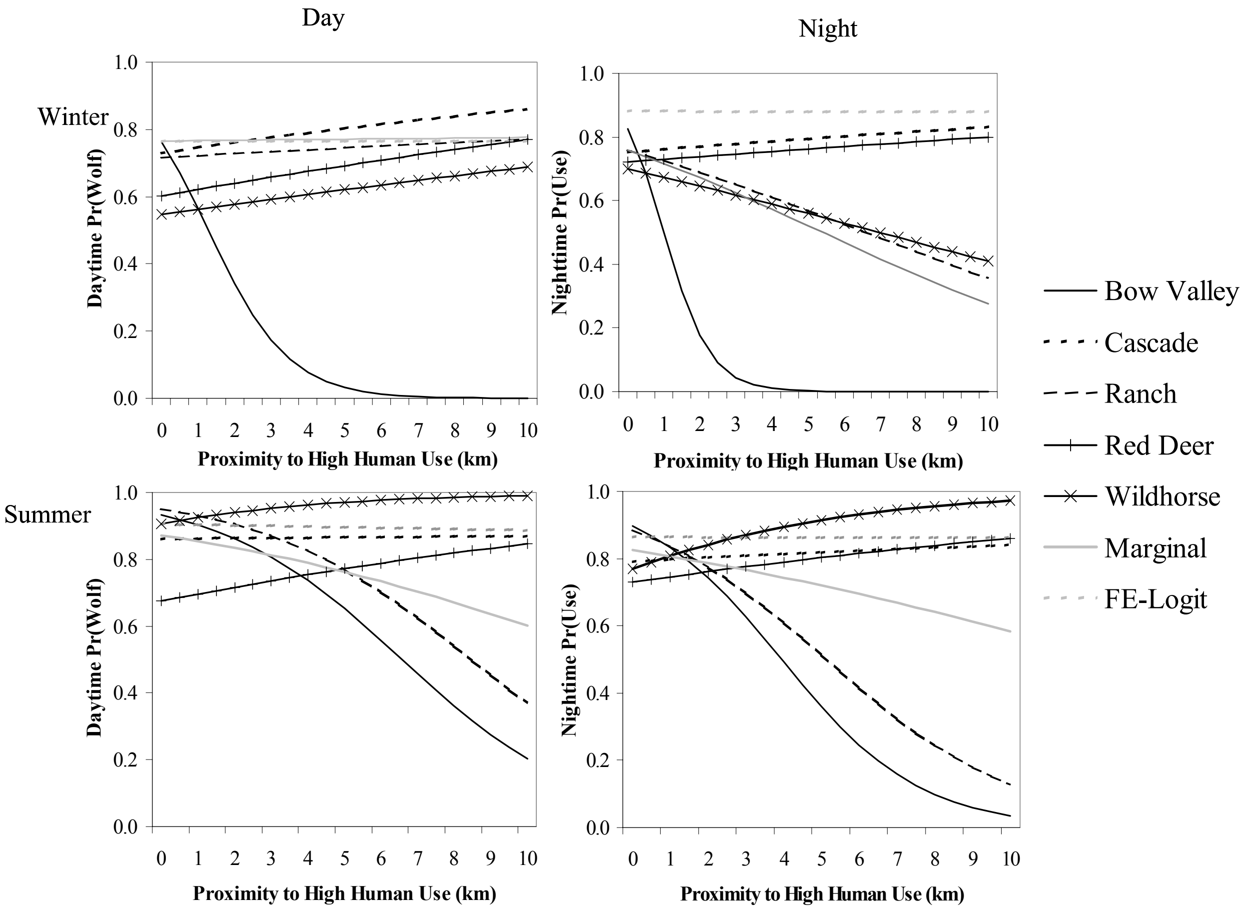


Fig. 4-1. Conditional predicted relative probabilities of use as a function of proximity to high human use seasonally and temporally for wolves in the eastern slopes of BNP, 2002-2004. Conditional predictions are given a specific pack holding all other effects constant. The marginal, or population-level prediction, and prediction from the naïve logit, are shown for comparison.

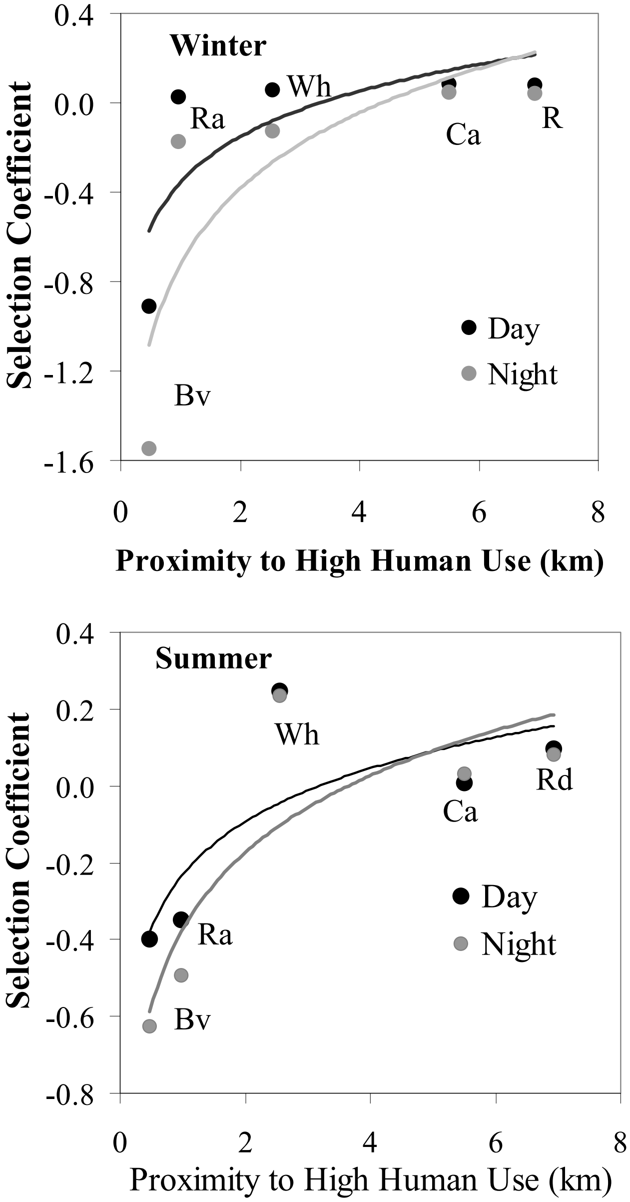


Fig. 4-2. Seasonal functional responses in resource selection by wolf packs (y-axis shows selection coefficient) as a function of changing seasonal home range proximity to high human use (x-axis) in the eastern slopes of BNP. Acronyms of wolf packs and functional response models are given in the text. See text for more details.

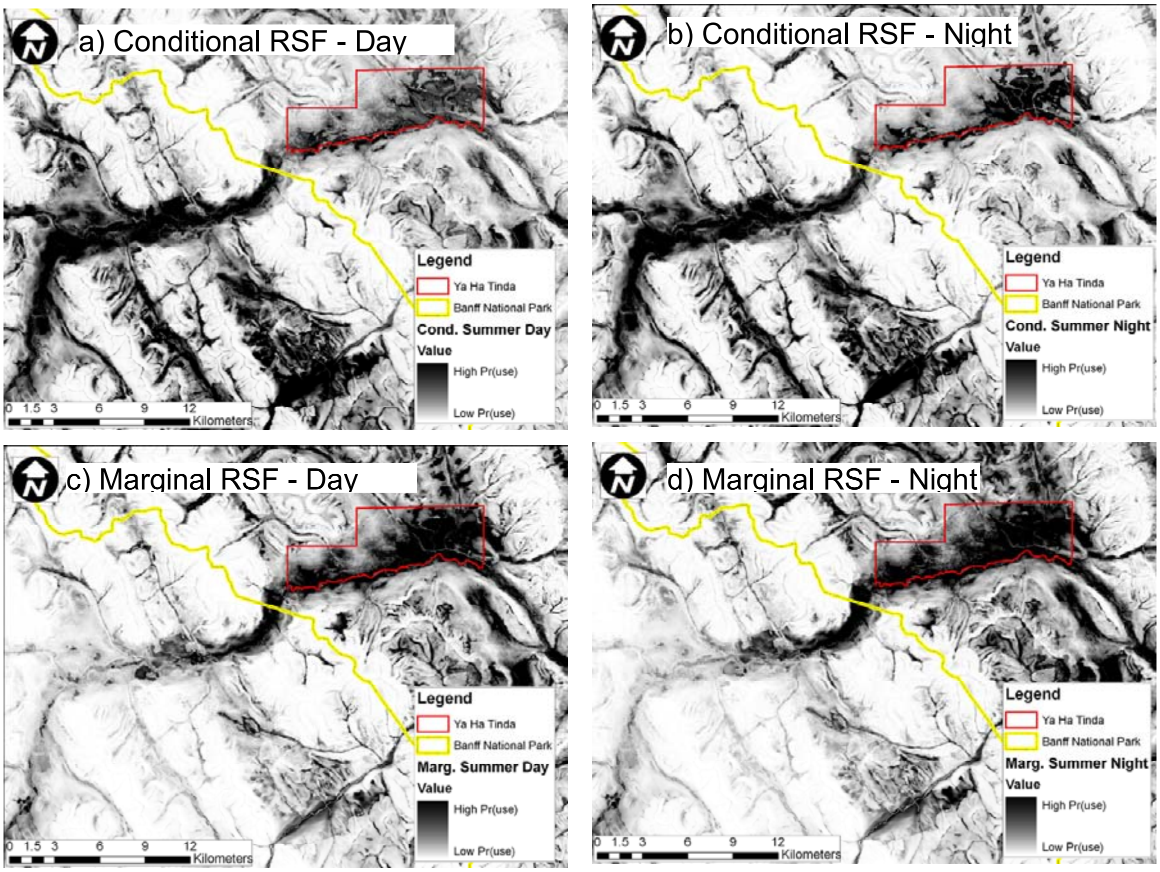


Fig. 4-3 Comparison of conditional (a&b) and marginal (c&d) inferences from 3-level mixed effects wolf RSF models during summer between night (b&d) and day (a&c). Probability of wolf use is scaled between 0 (low) and 1 (high). The YHT outside BNP has high human activity levels, whereas inside BNP the lowest human activity levels in the study area occur. Inferences differ between the marginal and conditional models across this gradient only in areas of high human use at the YHT ranch during summer via a spatio-temporal refuge from predation. See text for details.

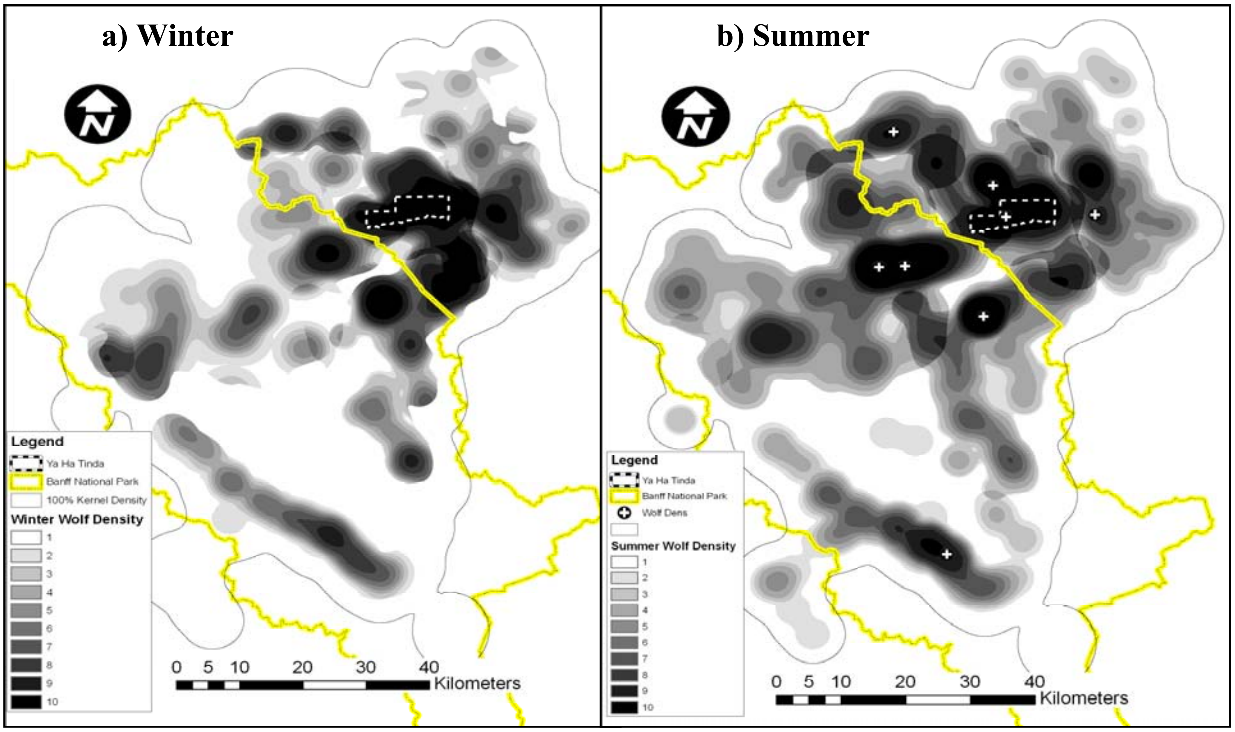


Fig. 4-4. Wolf probability density functions (PDF) weighted by average seasonal pack size combined across packs during a) winter and b) summer (showing active wolf den sites), 2002-2004. PDF’s were calculated for each pack, combined, and then weighted by average seasonal wolf pack size and reported as relative spatial density between 1 and 10.

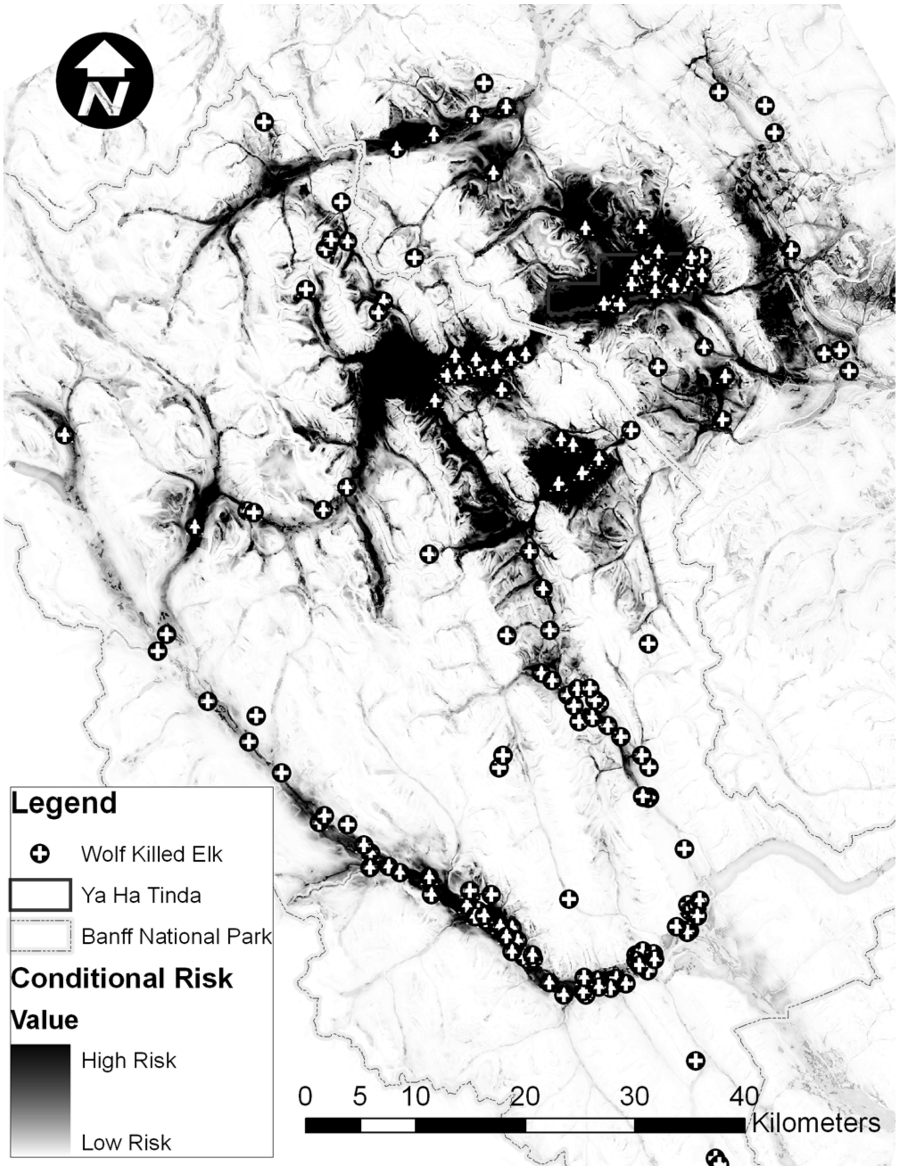


Fig. 4-5. Final total conditional wolf predation risk model during winter (average of both night and day) as a combination of spatial wolf density and pack-level wolf resource selection given a functional response to human activity (see text for details). Locations of the wolf-killed elk used to validate risk models for comparison.

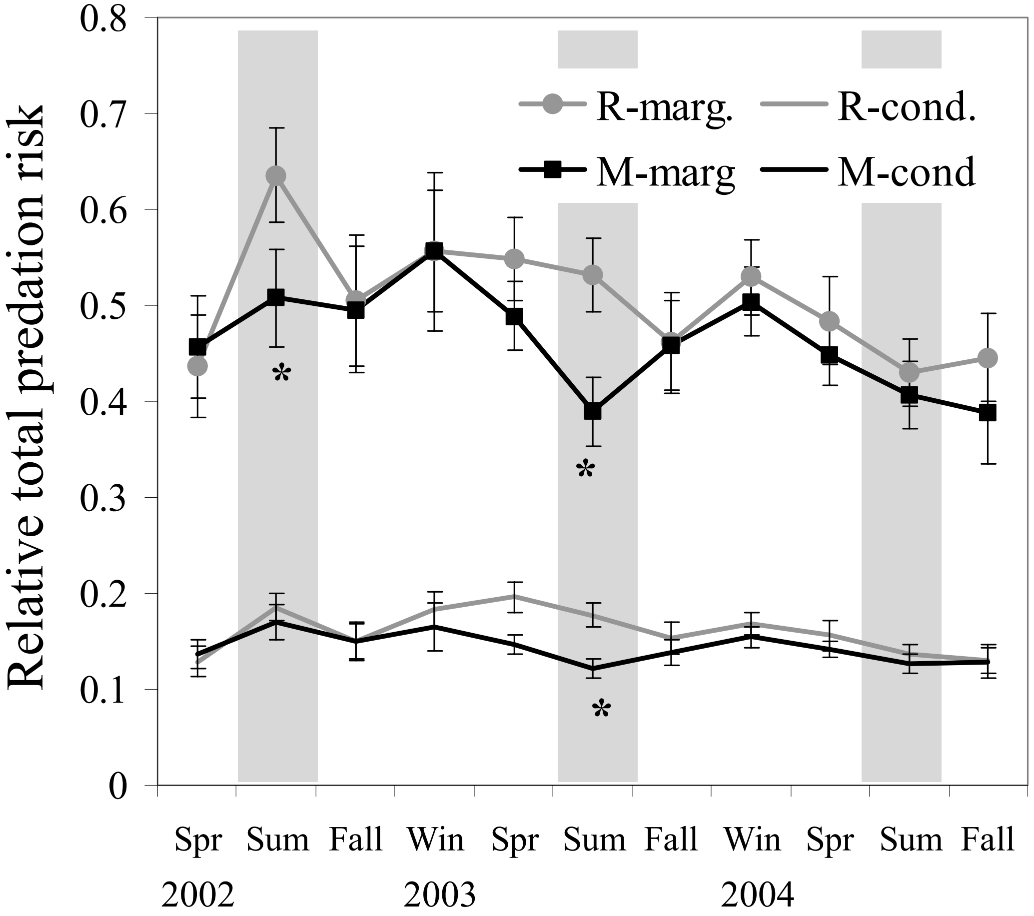


Fig. 4-6. Relative total predation risk for migrant (M) and resident (R) elk from marginal (marg) and conditional wolf predation risk functions in the partially migratory YHT elk herd, spring 2002 to Fall 2004. Mean predation risk averaged across individual elk is show with SE, and summer periods, during which benefits from migration were expected to accrue, are highlighted in shaded bars. Statistical differences between migrants and residents from a linear mixed effects model accounting for individual elk and autocorrelation across seasons are marked with a * (see text).

LITERATURE CITED

Baltagi, B.H. and P.X. Wu. 1999. Unequally spaced panel data regressions with AR(1) disturbances. Econometric Theory **15**:814-823.

Beale, C.M. and P. Monaghan. 2004. Human disturbance: people as predation-free predators? Journal of Applied Ecology **41**:335-343.

Begg, M.D. and M.K. Parides. 2003. Separation of individual-level and cluster-level covariate effects in regression of correlated data. Statistics in Medicine **22**:2591-2602.

Bergerud, A. T., Butler, H. E. and D.R. Miller. 1984. Antipredator tactics of calving caribou - dispersion in mountains. Canadian Journal of Zoology **62:** 1566-1575.

Bennington, C.C. and W.V. Thayne. 1994. Use and misuse of mixed-model analysis of variance in ecological-studies. Ecology **75**:717-722.

Bergman, E.J., R.A. Garrott, S. Creel, J.J. Borkowski, and R.M. Jaffe. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications In Press.

Beyer, H. 2005. Hawthtools analysis tools for ArcGIS. Edmonton, Alberta.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological modelling **157**:281-300.

Boyce, M.S. and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution **14**:268-272.

Boydston, E.E., K.M. Kapheim, H.E. Watts, M. Szykman, and K.E. Holekamp. 2003. Altered behaviour in spotted hyenas associated with increased human activity. Animal Conservation **6**:207-219.

Breslow, N.E. and D.G. Clayton. 1993. Approximate inference in generalized linear mixed models. Journal of the American Statistical Association **88**: 9-25.

Burcham, M., W.D. Edge, and C.L. Marcum. 1999. Elk use of private land refuges. Wildlife

Society Bulletin **27**:883-839.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Callaghan, C.2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival, and persistence in the Central Rocky Mountains, Canada. Department of Zoology, University of Guelph. Guelph, ON.

Cam, E., W.A. Link, E.G. Cooch, J.Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. American Naturalist **159**:96-105.

Caro, T.M. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, USA.

Ciucci, P., M. Masi, and L. Boitani. 2003. Winter habitat and travel route selection by wolves in the Northern Apennines, Italy. Ecography **26**:223-235.

Conradt, L., T.H. Clutton-Brock, and F.E. Guinness. 1999. The relationship between habitat choice and lifetime reproductive success in female red deer. Oecologia **120**:218-224.

Duke, D. L. 2001. Wildlife use of corridors in the Central Canadian Rockies: Multivariate use of habitat characteristics and trends in corridor use. Masters of Science, University of Alberta, Edmonton, Canada.

Duke, D. L., Hebblewhite, M., Paquet, P. C., Callaghan, C. and M. Percy. 2001. Restoration of a large carnivore corridor in Banff National Park. Large mammal restoration: ecological and sociological challenges in the 21st century, eds D. S. Maehr, R. F. Noss & J. L. Larkin, pp. 261-275. Island Press, Washington.

Forman, R.T.T. and L.E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29**: 207-240.

Fortin, D., H. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne, and J.S. Mao. 2005. Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. Ecology **86:** 1320-1330.

Franklin, S.E., G.B. Stenhouse, M.J. Hansen, C.C. Popplewell, J.A. Dechka, and D.R. Peddle. 2001. An integrated decision tree approach (IDTA) to mapping landcover using sattelite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. Canadian Journal of Remote Sensing **27**:579-592.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton.

Frid, A. and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**: 11-19.

Fryxell, J.M., J. Greever, and A.R.E. Sinclair. 1988. Why are migratory ungulates so abundant? The American Naturalist **131**: 781-798.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Research Techniques in Animal Ecology: Controversies and Consequences (eds L. Boitani & T. K. Fuller), pp. 111-154. Columbia University Press, New York.

Gibeau, M.L., A.P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the bow river watershed, Alberta, Canada. Biological Conservation **103**: 227-236.

Gillies, C., M. Hebblewhite, S.E. Nielsen, M. Krawchuk, C. Aldridge, J. Frair, C. Stevens, D.J. Saher, and C. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology, In Review.

Girard, I., J.P. Ouellet, R. Courtois, C. Dussault, and L. Breton. 2002. Effects of sampling effort based on gps telemetry on home-range size estimations. Journal of Wildlife Management **66**: 1290-1300.

Hayes, R. D., Farnell, R., Ward, R. M. P., Carey, J., Dehn, M., Kuzyk, G. W., Baer, A. M., Gardner, C. L. & O'donoghue, M. 2003. Experimental Reduction of Wolves in the Yukon: Ungulate Responses and Management Implications. Wildlife Monographs, 1-35.

Hebblewhite, M., E.H. Merrill, and T.E. McDonald. 2005a. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk system. Oikos 111:101-111.

Hebblewhite, M., C.A. White, C. Nietvelt, J.M. McKenzie, T.E. Hurd, J.M. Fryxell, S. Bayley, and P.C. Paquet. 2005b. Human activity mediates a trophic cascade caused by wolves. Ecology **86**: 2135-2144.

Hebblewhite, M., P.C. Paquet, D.H. Pletscher, R.B. Lessard, and C.J. Callaghan. 2004. Development and application of a ratio-estimator to estimate wolf killing rates and variance in a multiple prey system. Wildlife Society Bulletin **31**: 933-946.

Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. MacDonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggest problems for kernel home-range analyses with least-squares cross-validation. Journal of Animal Ecology **74**:455-463.

Hernandez, L. and J.W. Laundre. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk and bison. Wildlife Biology **11**:215-220.

Holland, W.D. and G.M. Coen. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 1: Summary. Alberta Institute of Pedology, Edmonton, AB.

Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European sawfly. The Canadian Entomologist **91**:293-320.

Holroyd, G.L. and K.J. Van Tighem. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 3. The wildlife inventory. Canadian Wildlife Service, Edmonton.

Hopcraft, J.G.C., A.R.E. Sinclair, and C. Packer. 2005. Planning for success: serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology **74**:559-566.

James, A.R.C.1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. Dissertation. University of Alberta.

Edmonton, Alberta.

Jevons, S. 2001. Human use digital atlas of the Canadian Central Rockies ecosystem. Miisitakis Institute for the Rockies & Geoworks GIS, Canmore, AB.

Johnson, C.J., K.L. Parker, D.C. Heard, and M.P. Gillingham. 2002. A multi-scale behavioural approach to understanding the movements of woodland caribou. Ecological Applications **12**:1840-1860.

Kaartinen, S., I. Kojola, and A. Colpaert. 2005. Finnish wolves avoid roads and settlements. Ann. Zool. Fennici **42**: 523-532.

Kauffman, M.J., N. Varlely, D.W. Smith, D.R. Stahler, D.R. MacNulty, and M.S. Boyce. In Review. Competition for optimal hunting grounds decouples predation risk from predator distribution in a wolf-elk system. Nature

Kjellander, P., J.M. Gaillard, M. Hewison, and O. Liberg. 2004. Predation risk and longevity influence variation in fitness of female roe deer. Proceedings of the Royal Society of London Series B-Biological Sciences **271**:S338-S340.

Kloppers, E. L., St Clair, C. C. and T.E. Hurd. 2005. Predator-resembling aversive conditioning for managing habituated wildlife. Ecology and Society, 10. [URL] http://www.ecologyandsociety.org/vol10/iss1/art31/

Kristan, W.B.I. and W.I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology **84**:2432-2443.

Lewis, M. A. and Murray, J. D. 1993. Modeling territoriality and wolf deer interactions. Nature **366:** 738-740.

Lima, S.L. and P.A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. Trends in Ecology and Evolution **11**:131-135.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Second Edition. Kluwer, Boston, USA.

Mauritzen, M., Belikov, S. E., Boltunov, A. N., Derocher, A. E., Hansen, E., Ims, R. A., Wiig, O. & Yoccoz, N. 2003. Functional responses in polar bear habitat selection. Oikos **100:** 112-124.

McInenly, L. E. 2003. Seasonal effects of defoliation on montane Rough Fescue *(Festuca campestris Rydb.)*. Masters of Science Thesis, University of Alberta, Edmonton, Canada.

McKenzie, J.A. 2001. The selective advantage of urban habitat use by elk in Banff National Park. University of Guelph. Guelph, Ontario.

Mech, L.D. and L. Boitani. 2003. Wolves. Behaviour, ecology, and conservation. University of Chicago Press, Chicago.

Mech, L.D., S.H. Fritts, G.L. Radde, and W.J. Paul. 1988. Wolf distribution and road density in Minnesota. Wildlife Society Bulletin **16**:85-87.

Merrill, S.B. 2000. Road densities and gray wolf habitat suitability: an exception. Canadian Field-Naturalist **114**:312-313.

Messier, F. 1995. On the functional and numeric responses of wolves to changing prey density. Pages 187-198 in L. N. Carbyn, S. H. Fritts, and D. R. Seip editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute,

Mladenoff, D.J., T.A. Sickley, R.G. Haight, and A.P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern great-lakes region. Conservation Biology **9**:279-294.

Musiani, M. and P.C. Paquet. 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. Bioscience **54**:50-61.

Mysterud, A. and R.A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology **79**:1435-1441.

Ogutu, J.O., N. Bhola, and R. Reid. 2005. The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. Journal of Zoology **265**: 281-293.

Osko, T.J., M.N. Hiltz, R.J. Hudson, and S.M. Wasel. 2004. Moose habitat preferences in response to changing availability. Journal of Wildlife Management **68**:576-584.

Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A.R.E. Sinclair. 2005. Ecological change, group territoriality, and population dynamics in serengeti lions. Science **307**: 390-393.

Paquet, P.C., Wierzchowski, J., and Callaghan, C. 1996. Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park. Pp 7-1-74 *in* J. C. Green, C. Pacas, L. Cornwall, and S. Bayley editors. Ecological Outlooks Project. A cumulative effects assessment and futures outlook of the Banff bow valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON.

Powell, R.A. 2000. Animal home ranges and territories and home range estimators. Pages 133-154 in L. Boitani and T. K. Fuller editors. Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York.

Rabe-Hesketh, S. and A. Skrondal. 2005. Multilevel and longitudinal modeling using STATA. Stata Corp, College Station, TX, USA.

Rabe-Hesketh, S., A. Skrondal, and A. Pickles. 2005. Maximum likelihood estimation of limited and disCrête dependent variable models with nested random effects. Journal of Econometrics **128**: 301-323.

Rettie, W.J. and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography **23**:466-478.

Schmitz, O. J., Beckerman, A. P. & O'Brien, K. M. 1997. Behaviourally mediated trophic cascades: effects of predation risk on food web interactions. Ecology **78:** 1388-1399.

Seip, D.R. 1992. Factors limiting woodland caribou populations and their relationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology **70**:1494-1503.

Skrondal, A. and S. Rabe-Hesketh. 2004. Generalized latent variable modeling: multilevel, longitudinal, and structural equation models. Chapman and Hall, New York, NY, USA.

StataCorp. 2003. Stata Statistical Software: Release 8.0. Stata Corporation, College Station, TX, USA.

Taylor, R. J. and Pekins, P. J. 1991. Territory boundary avoidance as a stabilizing factor in wolf-deer interactions. Theoretical Population Biology: **39** 115-128.

Ten Have, T.R., A.R. Kunselman, and L. Tran. 1999. A comparison of mixed effects logistic regression models for binary response data with two nested levels of clustering. Statistics in Medicine **18**:947-960.

Theuerkauf, J., W. Jedrzejewski, K. Schmidt, and R. Gula. 2003. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). Journal of Wildlife Management **67**:706-716.

Thiel, R.P. 1985. Relationship between road densities and wolf habitat suitability in wisconsin. American Midland Naturalist **113**:404-407.

Thurber, J.M., R.O. Peterson, T.D. Drummer, and T.A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin **22**:61-68.

Trinkel, M., P.H. Fleischmann, A.F. Steindorfer, and G. Kastberger. 2004. Spotted hyenas (*Crocuta crocuta*) follow migratory prey. Seasonal expansion of a clan territory in Etosha, Namibia. Journal of Zoology **264**:125-133.

White, C. A., Feller, M. C. and S.Bayley. 2003. Predation risk and the functional response of elk-aspen herbivory. Forest ecology and Management, **181:** 77-97.

White, C.A., C.E. Olmstred, and C.E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Widlife Society Bulletin **26**:449-462.

White, C., D. Gilbride, M. Scott-Brown, and C. Stewart. 1995. Atlas of the Central Rockies Ecosystem: Towards an Ecologically Sustainable Landscape. Komex International Ltd., Calgary.

Whittington, J., C.C. St Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications **15**:543-553.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology **70**:164-168.

Wyveden, A.P., D.J. Mladenoff, T.A. Sickley, B. Kohn, R.P. Thiel, and J.L. Hansen. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great lakes region. Endangered Species Update **18**:110-114.

CHAPTER FIVE

TRADE-OFFS BETWEEN WOLF PREDATION RISK AND FORAGE AT MULTIPLE-SCALES IN A PARTIALLY MIGRATORY UNGULATE.

INTRODUCTION

Ungulates consume plants and are consumed by predators, and must therefore adapt their behavioural and life history strategies to trade-offs between avoiding the risk of predation and gaining access to forage (Festa-Bianchet 1988, Kie 1999). Theoretical advances from small-scale experiments on risk–forage trade-offs (e.g., Gilliam and Fraser 1987) often provide limited understanding (Lima and Zollner 1996) for real environments because trade-offs can occur across a range of spatio-temporal scales (Lima 2002, Dussault et al. 2005). For example, migration is a large, landscape-scale strategy by which ungulates trade-off between risk and forage. Migration allows ungulates to 'escape' predation by moving beyond the ranges of non-migratory predators where they can 'relax' risk avoidance, and focus on maximizing benefits from forage while also enjoying reduced predation (Fryxell et al. 1988). While support for the benefits of migration to ungulates comes from both empirical and modeling studies, few have explicitly compared trade-offs between risk and forage. Instead, ecologists usually have focused on evaluating the foraging benefits of migration (Mysterud et al. 2001, Chapter 3), or alternatively, focused only on predation risk benefits of migration (Chapter 4, Bergerud et al. 1990).

Complete escape from predation, even by migrating across large spatial scales, is rare, for example, because migratory movements themselves can incur elevated risk (e.g., Lank et al. 2003, Schmaljohann and Dierschke 2005). Thus, at finer-scales, ungulates also also avoid predators by exploiting heterogeneity in predator distribution (i.e., refugia), temporally avoiding predator activity, or by reducing vulnerability to predators by grouping to dilute risk (Hamilton 1971, Caro 2005, Fortin et al. 2005, Hebblewhite et al. 2005,). Spatial-temporal avoidance at fine-scales may successfully reduce risk, but this strategy incurs a direct cost to foraging when risk and forage are positively correlated (Houston and McNamara 1993, Altendorf et al. 2001, Hernandez and Laundre 2005). Therefore the question becomes is it more advantageous to make trade-offs between risk and predation at larger spatial scales to avoid having to make finer-scale trade-offs where there might be a greater direct cost to foraging?

Few studies have directly addressed multi-scale trade-offs between forage selection and predator avoidance. Instead, previous studies often used proxies for forage or predation risk, such as snow depth, landcover types, or hiding cover (Mysterud et al. 1999, Johnson et al. 2002, Dussault et al. 2005). Progress has been limited by the difficulties of quantifying predation risk and forage for ungulates at landscape scales. These difficulties have hindered scaling-up ecologists understanding of forage-risk trade-offs to what Lima and Zollner (1996) called the 'behavioural ecology of ecological landscapes', critical to understanding many conservation problems. Recent advances in the ability to measure landscape-scale forage availability through remote sensing (Pettorelli et al. 2005), and to spatially model predation risk (Hebblewhite et al. 2005) provide new opportunities to address risk-forage trade-offs for ungulates at multiple scales relevant to ecosystem management (e.g., Lehmkuhl et al. 2001). For example, worldwide declines in migratory ungulate populations (Berger 2004), and controversies over efficacy of large-scale wolf (*Canis lupus*) controls to increase ungulate populations (Orians et al. 1997), depend on consequences of risk-forage trade-offs at landscape scales.

In this paper I examined multi-scale trade-offs in resource selection between herbaceous forage biomass (hereafter forage) and wolf predation risk (hereafter predation) for a partially migratory elk (*Cervus elaphus*) population in the Canadian Rockies using resource selection functions (RSF)(Manly et al. 2002). Contrasting trade-offs between migratory and non-migratory (resident) elk provided a powerful comparative design to understand how the spatial scale of selection influenced trade-offs. Both migrant and resident elk used the same winter range, so I focused here only on the summer migratory period. In Chapter 3, considering the effects of forage in isolation, I showed migrants selected areas with intermediate forage biomass, maximizing exposure to forage quality. In contrast, residents had lower overall exposure to forage quality and selected for areas with maximum forage biomass. These results were consistent with the forage maturation hypothesis explaining ungulate migration (e.g., Fryxell 1991), but failed to consider predation risk. Migrants also benefited from reduced predation risk, but residents partially mitigated higher risk by exploiting fine-scale predation refugia generated by wolf avoidance of humans (Chapter 4). That residents avoided risk at fine-scales suggests the potential for a trade-off cost between forage and predation for residents. Based on this, I hypothesized that migrants would select for forage independent of predation if they successfully avoided predation at the largest scales through migration. In contrast, I predicted residents would make fine-scale trade-offs between forage and predation, changing selection for forage under increasing predation (Houston and McNamara 1993, Pulliam 1983). To test the trade-off hypothesis, I compared migrant and resident resource selection for areas varying in forage biomass and predation risk using RSF's, first between home ranges (landscape-level) and then within home ranges (home-range level). I expected residents, but not migrants, would have a negative interaction of forage and predation at the within-home range scale, indicating their foraging strategy changed in areas of both high forage and predation. Further, I compared predation risk exposure of migrant elk during migratory movements to that on their summer ranges because this could be viewed as a cost to migration (Lank et al. 2003, Nicholson et al. 1997).

STUDY AREA

The study area is 7,000 km^2 in the eastern slopes of the Canadian Rockies in Banff National Park (BNP) and adjacent Alberta provincial lands. Wolves were the primary predator (Chapter 6) of a partially migratory elk population that migrated to summer ranges in mountainous areas of BNP, and wintered on the Ya Ha Tinda (YHT) ranch outside of BNP (Chapter 2, Morgantini et al. 1988). Human activity was concentrated on the YHT outside of BNP. Prescribed fires were a dominant landcover type, covering >200 km^2, and enhanced elk forage in the study area (Sachro et al. 2005). See Chapter 2 for more detailed information about the study area climate, vegetation, and ecology.

METHODS

Elk were captured using two corral traps (n=129) and helicopter netgunning (n=15) during winters 2002-2004. For this paper I used data from 109 adult female elk outfitted with 104 VHF and 27 GPS (some elk wore both) collars (LOTEK Ltd.) during the summer migratory period (1 June to 30 September, Chapter 2) from 2002–2004. Of the collared sample, 67 were migrants, and 44 residents. I collected VHF locations for collared elk from the air or ground every week, using only VHF collared elk with >10 locations/month. I screend GPS data to a consistent 2-hour relocation schedule. Both location error and fix-rate bias were low enough to not influence RSF models (see Appendix 3). For further details on elk capture and handling see Chapter 3.

Multi-scale trade-offs between forage and predation risk

I evaluated elk resource selection for forage, predation, and their interaction at two spatial scales during the summer migratory period. At the landscape scale, availability of forage and predation was compared between migrant and resident summer ranges. Within summer-ranges, I evaluated trade-offs between forage and predation using resource selection functions (RSF; Manly et al. 2002). I evaluated the success of these resource selection strategies in avoiding predation by comparing migrant and resident summer range exposure to predation risk. At the finest level, predation on migrant summer range and risk experienced during migration was compared. I first briefly describe methods to estimate forage and predation, but refer readers to the details in Chapters 3 and 4 for a full description.

Forage availability and wolf predation risk

The availability of herbaceous forage biomass to elk was modeled during 2002-2004 using a dynamic forage model based on ground- and remote-sensing approaches. I focused on herbaceous forage because differences in forage exposure between strategies were driven by herbaceous, not shrub, biomass (Chapter 3). I used stratified-random sampling (n=983 plots) to sample availability of herbaceous forage biomass (dried g/m^2 of forb and graminoid) at the peak of the growing season (4 August) within landcover types derived from LANDSAT-TM data (Franklin et al. 2001). I statistically modeled the peak of herbaceous forage (g/m^2) across the study area at a 30m^2 pixel resolution using the best predictive general linear models (GLM) of spatial covariates including landcover type. Next, forage growth was spatially modeled each year from the start (8 May) through the peak to the end of the growing season (15 October) using the Normalized Difference Vegetation Index (NDVI) from MODIS satellites (Huete et al. 2002) in open habitats in 16-day intervals, and plots (n=30) sampled ~3.5 times/season in closed habitats. I then combined the peak of forage biomass model with the forage growth model to create 16-day 'maps' of dynamic forage biomass availability between 8 May and 15 October at a 30m^2 pixel resolution. Note that elk forage selection is not necessarily governed solely by biomass because of digestive trade-offs between quality and quantity (Fryxell et al. 1991, Wilmshurst et al. 1995). Therefore, I interpreted forage biomass predictions from my dynamic forage models in terms of forage quality (% digestibility, Robbins et al. 1987, Hanley et al. 1992) using the seasonal relationship between forage biomass and quality in Chapter 3. All GIS analyses were done in ARCGIS 9.2 (ESRI Ltd).

Wolf predation risk was modeled by combining the summer resource selection patterns of wolves with their spatial density following Hebblewhite et al. (2005) in

Chapter 4. Summer resource selection patterns were estimated using locations (n= 12,521) from 11 GPS collared wolves from all five wolf packs that overlapped the YHT elk population from 2002-2004. Wolf predation risk was modeled using mixed-effects resource selection functions that allowed for pack-level heterogeneity in selection for human activity (Chapter 4). I used pack-level (conditional) risk instead of population-level (marginal) because pack-level best predicted locations of wolf-killed elk, and because of the pack-level wolf response to human activity (Chapter 4). Because wolves avoided linear features at the pack-level during the day in areas of high human activity, risk was modeled separately for night and day (Chapter 4). I then combined the seasonal-temporal wolf RSFs with their spatial density estimated based on a larger sample of 30 wolves using kernel density estimators (KDE, Worton 1989), weighed by an index of kill rate based on wolf pack size to model the total predation risk function for elk (Hebblewhite et al. 2005, Chapter 4).

Correlation between risk and forage

A crucial requirement for the existence of trade-offs between forage and predation is a positive correlation between both (Bowyer et al. 1998, Houston and McNamara 1993, Mitchell and Lima 2002). Without this correlation, foragers can simply maximize forage without considering predation. I assessed the relationship between predation and forage at elk telemetry locations and at random locations within elk summer ranges (see below) using Pearson's correlations.

Landscape-scale selection

An elk's decision to migrate reflects resource selection at the landscape scale. To assess resource selection at this scale, I compared availability of forage and predation between migrant and resident summer ranges for 109 GPS and VHF collared elk. For each elk I estimated one multi-annual 100% MCP summer range, and then summarized the summer range availability of these three risk measures within this 100% MCP using the zonal statistics function of Hawthtools 3.19 (Beyer 2005). To decompose effects of predation at this large scale, I contrasted elk exposure to the components of predation from Chapter 4: 1) total predation risk, 2) spatial wolf density (product of pack size and kernel density estimator) and 3) the wolf resource selection patterns at day and night. Forage availability early in the growing season (16 May) and during the peak of the growing season (5 August) was also compared across the home range between strategies. Differences between migrant and resident ranges for these multiple dependent variables were tested using MANOVA (StataCorp 2003). Variables were then tested individually for each covariate using a one-way ANOVA, correcting for multiple comparisons using the Bonferoni correction to evaluate the significance of the difference.

Home-range scale selection

I developed home-range scale RSF models using only GPS locations from 19 migrant and 8 residents during summer 2002-2004. I evaluated resource selection for forage, predation, and their interaction using the use-available design of Manly et al. (2002) where covariates at used and random locations were contrasted to estimate:

$$\hat{w}^*(x) = \exp(\hat{\beta}_1 F + \hat{\beta}_2 P + \hat{\beta}_n F * P) \quad (1)$$

where $\hat{w}^*(x)$ is the relative probability of use as a function of the coefficients $\hat{\beta}$ of forage (F), predation (P), and their interaction (F*P) estimated from fixed-effects logistic regression (Manly et al. 2002) in Stata 8.0 (StataCorp 2003). Random effects were included for individual elk to control for heterogeneity in resource selection and unbalanced sampling designs using GLLAMM in Stata 8.0 (Skrondal and Rabe-Hesketh 2004); see Chapter 4 for more detail on including mixed-effects in RSF models. I sampled availability for elk using 10 random points/km^2 within each 100% MCP summer home range. Because forage quality declined with increasing biomass, migrants maximized quality by selecting intermediate forage biomass. In contrast, residents selected for maximum forage biomass (Chapter 3). I accommodated these two different forage selection strategies in RSF models by including linear and quadratic (intermediate) selection functions. I also tested linear, quadratic and fractional polynomial (Hosmer and Lemeshow 2000) terms for predation, and tested for the forage-predation interaction on resource selection. The top model from the all-inclusive simple candidate set of forage, predation, their interaction, etc., was selected using AIC (Burnham and Anderson 1998). Predictive capacity was assessed using *k*-folds cross validation within 10 equal-interval bins of available relative probabilities (Boyce et al. 2002). I graphically represented the forage-predation interaction by estimating three deciles for predation and graphed the resultant probability of elk use as a function of forage.

Total predation risk exposure

To evaluate the success of resource selection strategies for avoiding risk, I assessed the exposure of all 109 elk to pack-level wolf predation risk during summers. Exposure to wolf predation risk (*Y*) was estimated using a linear mixed-effects model with a random-effect for each elk (Skrondal and Rabe-Hesketh 2004), a first-order autocorrelation term, and dummy variables for migratory status, the three summers of the study, and also interactions between migrant status and year (to test for annual differences between migratory strategies in each summer) using XTREGAR in STATA 8.0 (Baltagi and Wu 1999, StataCorp 2003) following

$$Y_{it} = \beta_0 + \beta_M X_{1i} + \beta_2 X_{2i} + \ldots + \beta_n X_{ti} + \boldsymbol{\beta_M X_t} + \gamma_i + \rho\varepsilon_{i,\, t\text{-}1} + \eta_{it} \tag{2}$$

where Y_{it} is P for elk i=1 during season t, β_M is the effect of migrant elk, $\beta_{2...t}$ are the seasonal coefficients (spring 2002, etc), $\boldsymbol{\beta_M X_t}$ is the vector of migrant*summer interactions, γ_i is the random effect of elk i, $\rho\varepsilon_{i,\, t\text{-}1}$ is the first-order autocorrelation term, and η_{it} is the random error. XTREGAR is robust to unbalanced observations in both i and t and seasonal gaps in t for i (Baltagi and Wu 1999). I used backwards-stepwise model selection to select the best predictive model.

Risk exposure during migratory movements

Finally, to test whether predation risk increased during migratory movements, I compared predation risk exposure during the spring and fall migratory periods to summer ranges for 18 GPS collared migrant elk. I first defined a 95% kernel home range for winter and summer for each migrant elk, and then defined locations between seasonal ranges as migratory movement locations (Craighead et al. 1972). Migratory movements were so rapid and definitive that this simple approach appeared satisfactory, and a more sophisticated approach failed to identify such movements (Johnson et al. 2002). I pooled spring and fall migratory movements and compared the mean migratory and summer period predation risk exposure for each elk using a paired t-test to test whether migration was riskier than when they were on their summer ranges.

RESULTS

Multi-scale trade-offs between forage and predation risk

Landscape-scale selection

Resident and migrant summer ranges differed for all eight covariates (MANOVA $F_{7, 102}$=30.31, P<0.0005, Wilks' λ=0.3455) even after adjusting for multiple comparisons (Table 5-1). Both spring and peak forage biomass were 30-40% lower on migrant summer ranges (Table 5-1) reflecting delayed phenology, and hence higher forage quality on migrant ranges (Chapter 3). Average wolf pack size between strategies did not differ during summer, but both their spatial density (KDE) and pack-size weighted KDE on migrant summer ranges was ~70% lower than residents, with only small resource selection risk differences during the night and day for migrants. In contrast, resident summer ranges were about 23% riskier at night than day. Combined, this translated into a 70% reduction in total wolf risk on migrant vs. resident summer ranges (Table 5-1).

Home range-scale selection

I used 2,762 VHF and 45,230 GPS locations from the 109 elk during summers 2002–2004 (Appendix 4) to develop resource selection functions. Forage biomass was correlated with predation risk at random locations throughout within elk summer ranges (r=0.37, *P*<0.0005) and at elk telemetry locations (r=0.41, *P*<0.0005). Despite the correlation, they were weaker than the guideline (r>0.70) for excluding collinear variables in logit models (Menard 2002). There was low model selection uncertainty for both the top migrant and resident models; the second ranked migrant and resident models both had low support, AIC weight = 0.14 and 0.07, respectively (Table 5-2). Because of this, I did not model average, and interpreted only the top model here. K-folds cross validation for five randomly selected partitions of the migrant and resident data had Spearman rank correlations of 0.86 (migrant model) and 0.94 (resident model) between observed and expected probabilities of use, indicating high predictive accuracy.

Migrant elk selected for intermediate levels of forage biomass regardless of the level of predation risk, with no forage-predation interaction. This indicated that as risk increased, migrants only reduced the strength of selection for a consistent intermediate forage biomass (Table 5-2, Fig. 5-1). In contrast, the top resident model had similar structure to the top migrant model, with intermediate selection for forage, but positive selection for predation in the presence of a strong negative interaction between predation and forage (Table 5-2). Under low predation, residents selected intermediate forage exactly the same as migrants (Table 5-2). However, as predation increased for residents, they changed their forage selection, switching to maximize forage (Fig. 5-1a).

Total predation risk exposure

From the top linear mixed effects model (XTREGAR Wald χ^2=14.85, p<0.007, $R^2_{overall}$ = 0.20, $R^2_{within\text{-}elk}$=0.30, $R^2_{between\text{-}elk}$=0.03, $\rho\varepsilon_{i,\,t-1}$=0.44), predation risk only differed between strategies during summer 2003 (β=-0.02, SE=0.005)(Fig. 5-2). Migration reduced risk by 9% in 2002, 29% in 2003, and 8% in 2004 relative to resident elk. On average, risk was reduced 15% by migration, but statistically significantly so only in one of three summers (Fig. 5-2).

Risk exposure during migratory movements

I identified 443 GPS locations as migratory movements from 17 GPS collared migrant elk for which there were $\geq$5 locations during migration. Each elk had an average of 23.5 GPS locations (range 5-149). Predation risk was 1.75 times higher during migratory movements ($\bar{x}$ = 0.201, SE=0.023) than on migrant summer ranges ($\bar{x}$ = 0.115, SE=0.015, Paired t-test $t_{\alpha=0.05/2,\ 16}$=-1.92, *P*=0.07) across all 17 elk, though 5 of the 17 elk had higher risk on summer ranges than during migration.

DISCUSSION

Elk that migrated avoided risk at the largest scales, eliminating the need to alter forage selection to minimize predation risk at finer-scales. At the fine scale, migrants were ‘free’ to focus on obtaining the highest diet quality by selecting areas of intermediate forage biomass. This was because migrants reduced predation risk 70% by moving farther from wolf denning areas compared to residents. This supported the prediction that at the fine-scale, migrants would not have to make trade-offs between forage and predation because overall, predation was very low. In contrast, resident elk summer ranges were much closer to wolf denning areas, and had much higher wolf predation risk as a result. Despite higher wolf use, resident elk switched their fine-scale foraging strategy to areas of highest rather than intermediate forage biomass. This allowed residents to mitigate their higher risk by only 15% higher, on average, than migrants (Chapter 4). Given the positive correlation between forage and predation, resident’s switch to select high forage under increasing predation was puzzling, because this strategy should have exposed elk to higher predation risk. Post-hoc exploration of forage–predation correlations at YHT provided an answer to this apparent paradox. Closer to human activity (< 0.68 km, the mean distance for elk to human activity), the strength of the forage–predation correlation was weaker (r= 0.21, P<0.005) than it was farther away (>0.68km) from human activity (r=0.51, P<0.0005). This allowed residents to relax risk avoidance and select for the higher forage present on the YHT grasslands, an area close to high human activity. The grasslands, with their high forage biomass, may facilitate larger group sizes because higher biomass may be required to minimize intra-specific foraging in large group sizes (Fortin et al. 2004). Larger group sizes would also contribute to reducing predation risk for residents (Hamilton 1971, Hebblewhite et al. 2002, Chapter 6). Further investigation will be needed to understand this spatial interaction between forage–predation and group size (Pierce et al. 2004, Chapter 6).

Because of delayed phenology on migrant ranges and the maximum forage quality expected at intermediate biomass (Chapter 3, Fryxell et al. 1991), selecting for intermediate biomass resulted in migrant exposure to forage that was ~5% higher digestibility than residents (Chapter 3). This difference is biologically significant enough to have important population consequences (Cook et al. 2004) and is consistent with higher pregnancy rates and calf weights of migrants reported in Chapter 6. In contrast, elk that did not migrate changed their forage selection strategies as predation hazard increased. Under low risk, resident elk followed a forage selection strategy similar to migrants by selecting intermediate forage biomass. As risk increased, however, residents switched their foraging strategy and selected for areas of maximum forage biomass. There were two factors reducing resident forage quality. First, the trade-off reported here that resulted in residents foregoing intermediate forage biomass with its higher forage quality. Second, resident summer ranges had lower forage quality overall because of large-scale phenological gradients (Chapter 3). Thus without the trade-off imposed by the avoidance of predation risk by residents, residents may still have incurred a lower average forage quality than migrants because of phenological differences. However, this trade-off undoubtedly exacerbated the overall poorer forage quality of residents, and combined, the two factors contributed to lower pregnancy rates and calf weights of resident elk (Chapter 6), suggesting potential costs to fitness. Where the interaction of these two factors may be of increased significance for residents is in combination with the effects of environmental stochasticity in winter severity, because in severe winters, their poorer forage quality may leave residents especially vulnerable.

Annual variation in the relative benefits of migration have important implications for the stability of partial migration (Kaitala et al. 1993). From an evolutionary perspective, variation in predation and forage increases the likelihood of coexistence of migrant and resident strategies (Kaitala et al. 1993). From a demographic perspective, temporal variation in predation has important implications for relative population growth rates between strategies (Boyce et al. 1991, Boyce and Anderson 1999). In female elk, which inherit migratory behaviour from their mothers, migratory strategy is often fixed, though some ‘switching’ occurs (e.g., Chapter 6). Over the lifespan (~20-years) of a female elk, migrants would therefore experience reduced predation. Resident elk, in contrast, would still be expected to have more years with high predation than migrants. How do residents persist given these benefits to migration? The answer may lie in the covariation between predation and and forage (Kaitala et al. 1993, Boyce and Anderson 1999). For example, in 2004, predation for residents was the lowest during the study, while forage was the highest (Chapter 3). High forage biomass may have allowed residents to ameliorate lower forage quality, and lower predation risk may have provided more flexibility to select for intermediate forage. Because predation and forage is already low for migrants, 2004 would therefore have been a relatively better year for residents than migrants. Thus, in this system, residents may be more sensitive to environmental stochasticity than migrants. Unfortunately, only a few other studies have examined demography of partially migratory ungulates for comparison. Nicholson et al. (1997) found migrant mule deer suffered higher mortality than residents in low precipitation years, but migrants had lower mortality in high precipitation (and hence forage) years. Thus, environmental stochasticity in forage availability balanced resident and migrant demography over time in this population, and was the mechanism maintaining partial migration for mule deer.

Risks incurred during migratory movements may also demographically balance strategies. The migratory period was the riskiest time of year for 70% of collared migrants, with risk elevated 1.7 times over the summer, higher even than resident elk (Fig. 5-3). This increase in risk during migratory movements was associated with a high frequency of mortalities caused by wolves (the leading cause of mortality) and grizzly bears (Chapter 6). Group sizes of elk were often smaller during migration than on summer ranges (*unpubl. data*), also increasing individual risk. Predation risk may influence how long it takes individuals to move through the area (Lank et al. 2003, Schmaljohann and Dierschke 2005). During this study, the duration of migratory movements of 17 GPS collared elk was <1 week, and averaged ~4 days (*unpubl.data*) both during fall and spring. Some migratory movements of >60km straight-line distances were made in <48 hours. In contrast, 25-years previous when wolves were rare or absent, Morgantini and Hudson (1988) documented extensive use of ‘intermediate’ ranges for periods up to months during the spring and fall. During my study, I did not observe migrant use of intermediate ranges, all of which were inside BNP in low elevation valley bottom areas of high predation risk. Instead, in this study, elk made rapid migratory movements. This indicates the duration of migration may have been reduced in response to wolf recolonization in this system.

My results do not completely support Rettie and Messier (2000)'s general hypothesis that ungulates avoid the most important limiting factors at the largest spatial scales, while focusing on secondary factors at finer scales. They showed that caribou avoided habitats with higher expected wolf predation risk at the largest spatial scales, focusing on foraging factors at finer scales, and interpreted this to mean wolf predation was the most limiting factor. In this study, migrant elk selected to avoid risk at the largest scale and selected intermediate forage at finer scales, in agreement with Rettie and Messier's (2000) hypothesis. However, by simultaneously avoiding predation risk and selecting for maximum forage biomass at fine-scales, residents did not make trade-offs between, but rather, within scales. This resident strategy was similar to that of moose in Quebec, where moose selected for both forage and predation risk at one scale (Dussault et al. 2005). Interestingly, in the case of residents, the decoupling of the correlation between risk and forage near human activity may have allowed them to make trade-offs at one scale. While this study revealed migrants and residents traded off between risk and predation at different scales, which strategy was more successful from a demographic perspective remains unknown. Therefore, consequences of hierarchical habitat selection by ungulates need to be evaluated from a demographic perspective, and the hypothesis that the most important limiting factors are selected for at the largest scale may not always be true. Indeed, Johnson et al. (2001) concluded that given behavioural flexibility of ungulates, there might be no inherent advantages to selecting forage or risk at any particular scale.

In summary, I showed that partially migratory elk adopted different strategies to avoid predation risk at landscape and home range scales that differentially influenced their foraging strategy. Migrant elk avoided predation risk at the landscape scale, allowing them to consistently select intermediate forage biomass at the fine-scale. Residents suffered 70% higher risk at landscape scales, but at least partially reduced risk at finer-scales using two mechanisms. First, resident elk changed their forage selection strategy in areas of high predation in a manner that suggests direct costs to foregoing higher forage quality. Second, residents exploited spatio-temporal refugia caused by wolf avoidance of high human activity areas during daytime to reduce risk (Chapter 4). As a consequence of these risk avoidance strategies, residents reduced their risk relative to migrants from 70% at the landscape scale to an overall 15% higher exposure to predation risk at the fine-scale. The combination of elevated risk during migration itself and the environmental stochasticity observed in migratory benefits in this study call into question whether the demographic benefits expected from migration exist in this partially migratory elk herd.

TABLE 5-1. Landscape-level resource selection differences in total wolf predation risk at the pack-level and its components, and herbaceous forage biomass (g/m^2) between migrant and resident elk summer ranges, 2002-2004.

	Migrant		Resident		Univariate ANOVA's†		
	Mean	StDev	Mean	StDev	F‡	P-value	r^2
N	67		44				
Wolf pack size††	11.4	6.79	13.8	6.09	5.2	0.062	0.09
Wolf KDE††	0.172	0.148	0.596	0.203	161.4	<0.0005	0.59
Spatial density††	0.466	0.392	1.631	0.544	171.5	<0.0005	0.61
Wolf RSF – Day	0.045	0.020	0.060	0.018	15.3	<0.0005	0.12
Wolf RSF – Night	0.040	0.017	0.074	0.033	48.4	<0.0005	0.31
Total wolf risk	0.037	0.036	0.129	0.065	112.8	<0.0005	0.46
Forage May 16 g/m^2	4.22	3.17	8.34	4.96	27.9	<0.00005	0.21
Forage Aug 5 g/m^2	10.63	4.96	17.11	7.17	31.15	<0.00005	0.23

Notes: Means are the average availability within the 100% summer range calculated using zonal statistics ++ in ARCGIS 9.2. Wolf predation risk RSF and total risk model is conditional at the pack-level. Overall MANOVA for covariates indicated significant differences between migrant and residents (see text for details).

† - Univariate ANOVA results for each covariate. P-value evaluated at an experiment-wise error rate adjusting for multiple comparisons of P=0.05/8 = 0.006.

‡ - All F-statistics at $df_1=1$, $df_2=109$.

††- Wolf pack size is the average number of wolves overlapping the elk home range, the wolf KDE is the spatial probability density function, and spatial density is the KDE weighted by wolf pack size (Chapter 4).

TABLE 5-2. Top RSF model selection results for within summer-range selection for forage (F), predation (P), and their interaction (F*P) for migrant and resident elk in the eastern slopes of Banff National Park, 2002-2004.

			Migrants			Residents		
Model name, structure		k	LL	ΔAIC	AIC *w*	LL	ΔAIC	AIC *w*
1) Migrant	$F+F^2+P$	4	-26,095	**0.0**	0.86	-13,356	5.3	0.07
2) Resident	$F+F^2+P+F*P$	5	-26,093	3.7	0.14	-13,351	**0.0**	0.93

Notes: the next closest model for both migrants and residents were > 380 ΔAIC units from these models, and are therefore not reported.

TABLE 5-3. Top model structure and diagnostics for migrant and resident summer-range RSF trade-off models between forage and risk of predation.

	Migrant		Resident	
Psuedo-R^2	0.11		0.28	
$n_{(0,1)}$	18736, 26417		8736, 26256	
K-folds spearman *r*	0.867		0.943	
Parameters	β	SE	β	SE
Forage (F)	0.064	0.001	0.074	0.001
Predation risk (P)	-1.671	0.122	1.816	0.217
F^2	-0.0004	1.06E-05	-0.0003	1.29E-05
F*P	---	---	-0.012	0.004

Notes: K-folds cross validation evaluate for 5 partitions of each dataset revealing good predictive accuracy between observed and expected predictions from RSF model (see text).

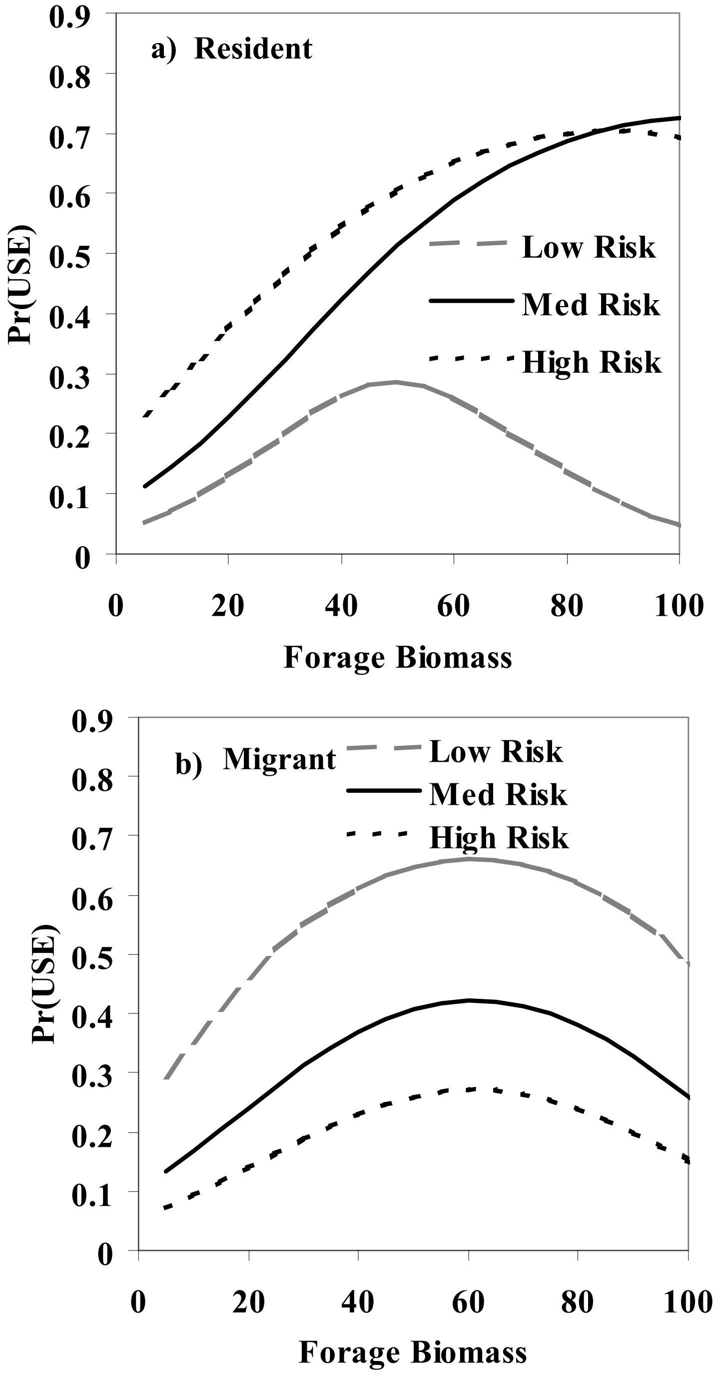


Fig. 5-1. Trade-offs in resource selection from forage-predation trade-off RSF models by resident (a) and migrant (b) elk for herbaceous forage biomass at low (0.01), medium (0.4), and high (0.75) levels of relative wolf predation risk (range 0-1). A negative trade-off between forage and risk is illustrated for residents, but not for migrants in the Ya Ha Tinda elk population, Banff National Park, Alberta.

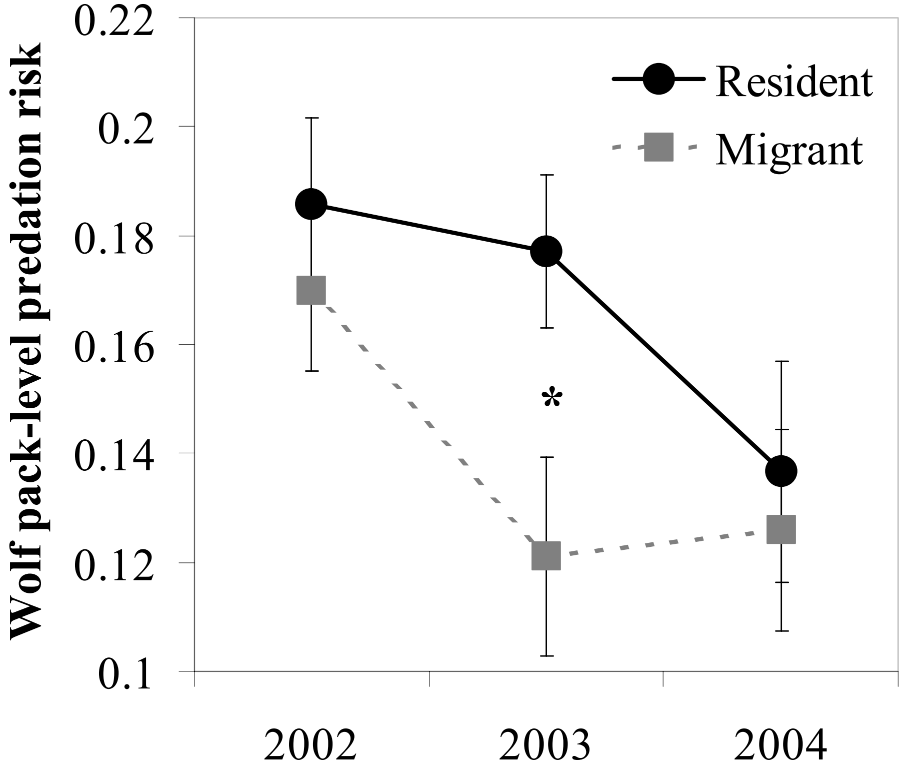


Fig. 5-2. Relative predation risk for migrant (M) and resident (R) elk from the partially migratory Ya Ha Tinda elk herd, summers (June 1 to Sept 30) 2002–2004. Mean predation risk averaged across individual elk is shown with SE’s. Statistical differences between migrants and residents from a linear mixed effects model accounting for individual elk and autocorrelation are marked with a * (see text). See text for a description of predation risk.

LITERATURE CITED

Albon, S.D. and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos **65**:502-513.

Altendorf, K.B., J.W. Laundre, C.A.L. Gonzalez, and J.S. Brown. 2001. Assessing effects of predation risk on foraging behaviour of mule deer. Journal of Mammalogy **82**:430-439.

Baltagi, B.H. and P.X. Wu. 1999. Unequally spaced panel data regressions with AR(1) disturbances. Econometric Theory **15**:814-823.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology **18,** 320-331.

Bergerud, A.T., R. Ferguson, and H.E. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behaviour **39**:360-368.

Beyer, H. 2006. Wolves, elk, and willow on Yellowstones northern range. Msc. Thesis. University of Alberta, Edmonton, AB, Canada.

Bowyer, R.T., J.G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy **79**:415-425.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological modeling **157**:281-300.

Boyce, M.S. 1991. Migratory behaviour and management of elk (*Cervus elaphus*). Applied Animal Behaviour Science **29**:239-250.

Boyce, M. S. and Anderson, E. M. 1999. Evaluating the role of carnivores in the Greater Yellowstone Ecosystem. Pages 265-284 In Clark, T.W., Curlee, A.P., Minta, S.C., and P. M. Kareiva (eds), Carnivores in Ecosystems: The Yellowstone Experience. Yale University press, New Haven and London.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Caro, T.M. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, USA.

Conradt, L., T.H. Clutton-Brock, and F.E. Guinness. 1999. The relationship between habitat choice and lifetime reproductive success in female red deer. Oecologia **120**:218-224.

Craighead, J.J., G. Atwell, and B.W. O'Gara. 1972. Elk migration in and near Yellowstone National Park. Wildlife Monographs **29**: 1-49.

Dussault, C., Ouellet, J P., Coutois, R., Huot, J., Breton, L. & Jolicoeur, H. 2005. Linking moose habitat selection to limiting factors. Ecography **28** 1-10.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia **75**:580-586.

Fortin, D., H. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne, and J.S. Mao. 2005. Wolves influence elk movements: behaviour shapes a trophic cascade in Yellowstone National Park. Ecology **86:** 1320-1330.

Fortin, D., Boyce, M. S. & Merrill, E. H. 2004. Multi-tasking by mammalian herbivores: overlapping processes during foraging. Ecology **85,** 2312-2322.

Franklin, S.E., G.B. Stenhouse, M.J. Hansen, C.C. Popplewell, J.A. Dechka, and D.R. Peddle. 2001. An integrated decision tree approach (IDTA) to mapping landcover using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. Canadian Journal of Remote Sensing **27**:579-592.

Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist **138**:478-498.

Fryxell, J.M., J. Greever, and A.R.E. Sinclair. 1988. Why are migratory ungulates so abundant? The American Naturalist **131**:781-798.

Gilliam, J.F. and D.F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology **68**:1856-1862.

Hamilton, W.D. 1971. Geometry for the selfish herd. Journal of Theoretical Ecology **31**:295-311.

Hanley, T.A., C.T. Robbins, A.E. Hagerman, and C. McArthur. 1992. Predicting digestible protein and digestible dry-matter in tannin-containing forages consumed by ruminants. Ecology **73**: 537-541.

Hebblewhite, M., E.H. Merrill, and T.E. McDonald . 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk system. Oikos **111**: 101-111.

Hebblewhite, M. and D.H. Pletscher. 2002. Effects of elk group size on predation by wolves. Canadian Journal of Zoology **80**:800-809.

Hebblewhite, M., C.A. White, C. Nietvelt, J.M. McKenzie, T.E. Hurd, J.M. Fryxell, S. Bayley, and P.C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology **86**:2135-2144.

Hernandez, L. and J.W. Laundre. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of Elk (*Cervus elaphus*) and Bison (*Bison bison*). Wildlife Biology **11**:215-220.

Hosmer, D.W. and S. Lemeshow. 2000. Applied Logistic Regression. John Wiley and Sons, New York.

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X. and Ferreira, L. G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment **83:** 195-213.

Johnson, C.J., K.L. Parker, D.C. Heard, and M.P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71: 225-235.

Johnson, C. J., Parker, K. L. & Heard, D. C. 2001. Foraging across a variable landscape: behavioural decisions made by woodland caribou at multiple spatial scales. Oecologia **127:** 590-602.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American

Naturalist **142**:59-81.

Kie, J.G. 1999. Optimal foraging and risk of predation: effects on behaviour and social structure in ungulates. Journal of Mammalogy **80**:1114-1129.

Kjellander, P., J.M. Gaillard, M. Hewison, and O. Liberg. 2004. Predation risk and longevity influence variation in fitness of female roe deer (*Capreolus capreolus*). Proceedings of the Royal Society of London Series B-Biological Sciences **271**:S338-S340.

Kristan, W.B.I. and W.I. Boarman. 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology **84**:2432-2443.

Lehmkuhl, J.F., J.G. Kie, L.C. Bender, G. Servheen, and H. Nyberg. 2001. Evaluating the effects of ecosystem management alternatives on elk, mule deer, and white-tailed deer in the interior Columbia River basin, USA. Forest ecology and management **153**:89-104.

Lank, D. B., Butler, R. W., Ireland, J. & Ydenberg, R. C. 2003. Effects of predation danger on migration strategies of sandpipers. Oikos **103:** 303-320.

Lima, S.L. 2002. Putting predators back into behavioural predator-prey interactions. Trends in Ecology and Evolution **17**:70-75.

Lima, S.L. and P.A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. Trends in Ecology and Evolution **11**:131-135.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Second Edition. Kluwer, Boston, USA.

Menard, S. 2002. Applied logistic regression. Second Edition. Sage Publications, London.

Mitchell, W.A. and S.L. Lima. 2002. Predator-prey shell games: large-scale movement and its implications for decision making by prey. Oikos **99**:249-259.

Morgantini, L.E. and R.J. Hudson. 1988. Migratory patterns of the wapiti, *Cervus elaphus*, in Banff National Park, Alberta. Canadian Field Naturalist **102**:12-19.

Mysterud, A., R. Langvatn, N.G. Yoccoz, and N.C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology **70**:915-923.

Mysterud, A., Lian, L. B. and Hjermann, D. O. 1999. Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. Canadian Journal of Zoology **77:** 1486-1493.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy **78**:483-504.

Orians, G., P.A. Cochran, J.W. Duffield, T.K. Fuller, R.J. Gutierrez, W.M. Henemann, F.C. James, P. Kereiva, S.R. Kellert, D. Klein, B.N. McLellan, P.D. Olson, and G. Yaska. 1997. Wolves, bears, and their prey in Alaska. National Academy Press, Washington.

Pettorelli, N., J.O. Vik, A. Mysterud, J.-M. Gaillard, C.J. Tucker, and N C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution **20**:503-510.

Pierce, B.M., R.T. Bowyer, and V.C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management **68**:533-541.

Pulliam, H.R. 1989. Individual behaviour and the procurement of essential resources. Pages 25-38 in J. Roughgarden, R. M. May, and S. A. Levin editors. Perspectives in ecology. Princeton University Press, Princeton, USA.

Rettie, W. J. and Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography **23:**466-478.

Robbins, C.T., S. Mole, A.E. Hagerman, and T.A. Hanley. 1987. Role of tannins in defending plants against ruminants - reduction in dry matter digestion. Ecology **68**:1606-1615.

Sachro, L.L., W.L. Strong, and C.C. Gates. 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Environmental Management **77**:183-193.

Schmaljohann, H. & Dierschke, V. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears. Journal of Animal Ecology **74**: 131-138.

Skrondal, A. and S. Rabe-Hesketh. 2004. Generalized latent variable modeling: multilevel, longitudinal, and structural equation models. Chapman and Hall, New York, NY, USA.

StataCorp. 2003. Stata Statistical Software: Release 8.0. Stata Corporation, College Station, TX.

Wilmshurst, J.F., J.M. Fryxell, and R.J. Hudson. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). Behavioural Ecology **6**:209-217.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology **70:** 164-168.

CHAPTER SIX

COMPARATIVE DEMOGRAPHY OF A PARTIALLY MIGRATORY ELK POPULATION: CONSEQUENCES OF TRADE-OFFS BETWEEN FORAGE AND PREDATION

INTRODUCTION

Migration is thought to have evolved as a fitness-maximizing strategy in the face of temporal (seasonal, annual) and spatial variation in resources (Swingland and Greenwood 1983, Baker 1978, Boyce 1991). By migrating, animals track fluctuating forage resources over large areas (Baker 1978, Swingland and Greenwood 1983) and can escape regulation by predators (Fryxell et al. 1988). Partial migration, where some individuals migrate and some are non-migratory, is possible where, for some proportion of the population, foregoing migration provides equal fitness to migrants (Baker 1978, Lundberg 1988). Partial migration is hypothesized to be maintained by the coexistence of migrant and resident strategies in a mixed evolutionary stable strategy (ESS), whereby the proportion of each strategy is described by an evolutionary stable state (ESSt) (Lack 1968, Lundberg 1988). Three main mechanisms have been proposed for the maintenance of an ESSt for the proportion of migrant and resident strategies (Lundberg 1988, Kaitala et al. 1993). First, animals can adaptively switch between migration (M) or resident (R) strategies, for example, as population density changes (Lack 1968, Berthold 2001). Second, animals can adopt a state-dependent M or R strategy dependent on their age or body condition (e.g., Adriaensen and Dhondt 1990, Perez-Tris and Telleria 2002). These first two mechanisms are both individual-based mechanisms, maintained either by genetic or phenotypic polymorphism (Lundberg 1988), where one strategy makes the 'best of a bad situation' (e.g., Adriaensen and Dhondt 1990). The third mechanism is a mixed 'population-level' ESSt where individuals are born as M or R, but proportions are fixed at the population level by density-dependent fitness balancing between strategies (Swingland and Lessells 1979, Lundberg 1988,).

Ecologist's understanding of partial migration comes predominately from studies on passerines (Lundberg 1988), yet partial migration is surprisingly common in other taxa such as large ungulates, including elk (*Cervus elaphus*)(Woods 1991), moose (*Alces alces*)(Andersen 1991, Ball et al. 2001,), mule deer (*Odocoileus hemionas*)(Nicholson et al. 1997), white-tailed deer (*O. virginianus*)(Forbes and Theberge 1995), and wildebeest (*Conochaetes taurinus*)(Fryxell et al. 1988). Evolution of partial migration in ungulates appears most consistent with a population-level mixed ESS, first, because ungulates show high fidelity to migratory strategies with little evidence for state-dependence (e.g., Nicholson et al. 1997). Secondly, ungulates show strong transmission of behaviour between parents and young including migration (e.g., migratory calving site fidelity, Bergerud et al. 1984, Van Dyke et al. 1998), suggesting maintenance of migratory behaviour through phenotypic polymorphism (Geist 1982). With the exception of a handful of studies (e.g., Andersen et al. 1990, Nicholson et al. 1997), few studies have examined demographic regulation of partial migration in ungulates despite its widespread prevalence. Instead, most studies show only that migration provides either access to high forage quality and/or reduced predation risk (Bergerud et al. 1984, Fryxell et al. 1988, Fryxell 1991, Albon and Langvatn 1992, Chapter 3, 4). While these studies may show the benefits of migration, they do not reveal how partial migration is maintained in ungulates.

Because of the aforementioned benefits of migration to ungulates, partial migration would be expected only where non-migratory (resident) individuals adopt life-history or behavioural tactics to minimize the relative demographic costs of foregoing migration. Residents could mitigate losses from foregoing migration by selecting riskier habitats with higher forage payoffs, or alternately, by avoiding risky habitats and making demographic trade-offs such as between adult survival and reproduction (Pulliam 1989, Houston et al. 1993). In Sweden, migrant moose may have benefited from reduced human hunting pressure, although at the expense of lower forage and calf survival (Ball et al. 2001, Andersen 1991). Migratory giant tortoises benefited from increased forage and reproduction, but at the cost of decreased adult survival relative to residents (Swingland and Lessels 1979). Furthermore, trade-offs also may be mediated by environmental stochasticity. For example, Nicholson et al. (1997) showed that in low precipitation years (and hence low forage production), survival of migrant mule deer was lower than residents, but in normal years, migrant survival was higher.

The purpose of this study was to assess the demographic consequences of partial migration in an elk population that wintered adjacent to Banff National Park (BNP) in the Canadian Rockies. Over the past 20-years, the proportion of residents in the population increased suggesting the demographic, and hence fitness, balance was in favor of residents (Chapter 2). By migrating to remote, high elevation summer ranges in BNP, migrant elk increased access to high forage quality (Chapter 3), and reduced exposure to predation risk (Chapter 4) except during migratory movements between seasonal ranges

(Chapter 5). In contrast, resident elk had a shorter duration of exposure to high quality forage (Chapter 3), and were faced with higher predation risk on summer ranges, yet they successfully reduced their risk by exploiting fine-scale refugia caused by wolf avoidance of human activity (Chapter 4, Hebblewhite et al. 2005). Therefore, I hypothesized that the demographic benefits from exploiting fine-scale spatial refugia compensated for poorer forage exposure and was sufficient to increase resident elk fitness relative to migrants in this system, switching the fitness balance in favour of residents.

To test this hypothesis, I compared vital rates and population growth rate (λ) between migrants and residents. Adult female survival was investigated using non-parametric Kaplan-Meier estimators (Cleves et al. 2003) to estimate survival rates, and using parametric Cox-proportional hazards survival models (Andersen and Gill 1990, Therneau and Grambsch 2000) to evaluate the effects of predation risk, forage, their interaction, and elk group size on adult survival. I then estimated calf survival using mark-resighting techniques (e.g., Testa 2004b). Demographic balancing could also occur through reproductive rates because of the trade-off between adult female and calf survival under heavy predation pressure (Testa 2004a). Therefore, I explored differences in pregnancy rates and reproductive pauses between M and R (Testa 2004a). Finally, vital rates were combined in a simple age-structured Leslie matrix model to compare relative fitness between strategies. I defined fitness as the strategy-specific population growth rate, lambda λ (Caswell 2001). I used the ratio of migrant and resident λ's to estimate the rate of change in fitness between strategies, equivalent to the rate of change in the M:R ratio in the population (Kaitala et al. 1993). I explored the sensitivity of λ to variation in vital rates using both deterministic and stochastic approaches to test how stochasticity may influence long-term stability between strategies in this population. While I assumed each migratory strategy was fixed in the demographic analyses, I estimated annual switching rates between strategies to test this assumption.

STUDY AREA

The study area lies on the eastern slopes of the Canadian Rockies ecosystem (White et al. 1995) in BNP and the province of Alberta. The study was conducted from February 2002 to November 2004 in a 7,000-km^2 area defined by the movements of the Ya Ha Tinda (YHT) elk population. Elk were the most abundant ungulate (White et al. 1995) and the dominant prey of wolves, which were in turn elk's main predator (Hebblewhite et al. 2004). Other prey species, in approximate order of relative abundance, included bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionas*), white-tailed deer (*O. virginanus*), mountain goats (*Oreamnos americanus*), moose (*Alces alces*), and a remnant herd of 5-8 mountain caribou (*Rangifer tarandus*). Other predators included grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Felis concolour*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*).

Almost the entire elk (95%) population winters at the YHT winter range. During summer, migrants move to summer ranges 20-60 km distant while residents remain on the YHT year-round. Historically, the proportion of migrants in this population approached 100%, but has recently declined to nearly 50% (Morgantini 1988, Chapter 2). While heavy bull harvests have been a historic feature of elk management, a short-term female hunting season of <=30 female elk occurred only from 1999 to 2003, overlapping with the period of study (Chapter 2, AB Fish and Wildlife, unpubl.data). For more details about the study area see Chapter 2.

METHODS

Elk Capture and Monitoring

I captured and handled 352 elk during winter (15 January to 31 March) from 2002-2004 at the YHT winter range (U. of Alberta Animal Care Protocol #353112) using two corral traps baited with alfalfa hay; elk were handled without chemical immobilization. Of these 352 elk, I randomly outfitted 109 female elk (≥yearling age) with VHF or GPS radiocollars (LOTEK Ltd.). Additionally, 11 elk were captured via helicopter netgunning to deploy collars. I deployed 32 GPS and 120 VHF collars, with some elk wearing both types consecutively. Capture bias appeared slight (+9%) for migrant elk but negligible in terms of spatial bias of summer range locations of migrant elk (Chapter 2, unpublished report). Rather than pull incisors to age elk (Festa-Bianchet et al. 2002), female elk were aged into four age classes based on tooth eruption, body weight, and capture history (i.e., those captured as calves). I classified elk as calves, yearlings (<1.5 to 2.5 years), subadults (<2.5 years) and adults (>2.5 years). Body mass of elk was recorded using a livestock scale and a body condition index was recorded under veterinary direction (Cook et al. 2001).

I monitored GPS and VHF elk aerially or from the ground a mean and median of once every 9.0 (SD = 11.13) or 6.0 days, respectively, until death, emigration, or the end of the study. GPS collar locations collected every 2-hours were resampled to 6-day intervals equivalent to VHF telemetry for survival analyses to ensure consistent sampling between migrant strata (Chen 2002, Frair 2005). Mean VHF location error was 218m (Appendix 3): using the Bessel function to model GPS error revealed 50% of the locations were within 34m of the true location, and 95% were within 113m (Appendix 3).

Habitat-induced GPS bias was low enough (<10%, Appendix 3) to be unimportant for habitat analyses (Frair et al. 2004). I defined migrant and residents by discriminating movements between non-overlapping seasonal summer ranges with VHF and GPS telemetry (Craighead et al. 1972). I estimated between-year switching rates between migratory strategies for 2003-2005 based on individuals with known migratory history monitored for 2 or more years.

Adult Female Survival

I investigated all mortalities 5.2 (SD = 7.98) days after detecting VHF mortality signals, and ascribed cause of death to predator (wolf, grizzly, other), human hunting, disease, or unknown causes following systematic criteria (e.g. Gauthier and Larsen 1986). I compared cause-specific mortality between migratory strategies using contingency tables. I summarized timing of mortality to investigate links to migration. Deaths within 1 month of capture (n=2) were considered to be caused by capture myopathy (Beringer et al. 1996) and censored. All but two mortalities (hunter kills) had known mortality date and location. For these two, I used the last known location in Cox-survival modeling (see below).

Survival rates

I used non-parametric Kaplan-Meier (K-M) survival analysis (Therneau and Grambsch 2000, Cleves et al. 2002) to estimate annual survival rates of residents and migrants for two full biological years, 2003 and 2004, from 2002 to 2004. Because biological years started June 1, I also estimated seasonal survival rates for the beginning and end of the study (see Table 6-1). Differences between migrant and resident survival rates were tested using the log-rank test (Cleves et al. 2002), and average annual cause-specific mortality rates calculated from K-M estimators.

Survival factors

I modeled risk factors influencing survival using the parametric Cox-proportional hazards model (Cox 1972, Andersen and Gill 1982, Therneau and Grambsch 2000) following:

$$h(\mathrm{t}|\mathrm{x}_\mathrm{j}) = h_0(\mathrm{t}) \exp(\mathbf{X}_\mathrm{j}\boldsymbol{\beta}_\mathrm{x} + \varepsilon) \qquad \textbf{(Eq.1)}$$

where $h(\mathrm{t}|\mathrm{x}_\mathrm{j})$ is the hazard for the *j*th elk, $h_0(\mathrm{t})$ is the baseline hazard, and $\mathbf{X}_\mathrm{j}\boldsymbol{\beta}_\mathrm{x}$ is the vector of risk covariates, X, for elk *j* and their coefficient, β. I tested the proportional hazard assumption for strategies and seasons using Schoenfeld residual plots and graphical methods (Therneau and Grambsch 2000, Cleves et al. 2002). If models violated the proportional hazards assumption, I attempted to meet assumptions by transformation, adding time or seasonal covariates (e.g., winter), or finally, through stratification (e.g. migrant, resident) in the Cox proportional hazard model (Therneau and Grambsch 2000, Cleves et al. 2002). I assessed the correct form of the covariates using Martingale residual plots (Therneau and Grambsch 2000, Cleves et al. 2002). I assessed goodness of fit (GOF) for the top selected model(s) using the Schoenfeld- test, and by testing for a 1:1 slope between the partial Cox-Snell residuals and the Nelson-Aalen cumulative hazard (Therneau and Grambsch 2000). Finally, to explore temporal patterns, the smoothed hazard was compared between migrants and residents (Cleves et al. 2002).

Validating survival models has not received much attention in the literature (Hosmer and Lemeshow 1999). I validated the predictive capacity of the final Cox-survival model using a validation procedure developed by Frair (2005) that compared the expected mortality frequencies to observed daily hazard rates. For each elk, I estimated the daily hazard as the sum of the daily-predicted hazard ratios (e.g., Eq. 1) divided by the total number of days each elk was alive. I then created 10 “bins” of relative daily hazard rates with equal numbers of elk. The frequency of mortalities in each bin was tallied, with the prediction, given a good model, that mortality frequency was positively related to the ranked relative daily hazard rate. I tested this prediction using Spearman’s rank correlation.

Model building and selection strategy

Because I had relatively small numbers of mortalities, the effective sample unit in survival models (Hosmer and Lemeshow 1999), I considered an all-inclusive set of candidate models consisting of the following four time-varying covariates: herbaceous forage biomass (g/m^2), wolf predation risk, their interaction, and elk group size. I explored strategy-specific effects by interacting these four covariates with a dummy variable for migrants and residents. I selected the top model using AICc (Burnham and Anderson 1998) where the sample size was number of deaths (Hosmer and Lemeshow 1999) and the number of parameters was the number of covariates + 1 for $h_0(t)$ and +1 for stratum (Therneau and Grambsch 2000).

Quantifying elk exposure to forage resources

I modeled the availability of herbaceous forage to elk using a dynamic forage model based on ground- and remote-sensing approaches in a Geographic Information System (GIS) using ARCGis 9.2 (Chapter 3). Herein I focus solely on herbaceous biomass because in Chapter 3 I showed that herbaceous forage drove differences in forage quality between strategies. Briefly, herbaceous forage biomass (dried g/m^2 of forb and graminoid) at the peak of the growing season (August 4) was sampled using stratified-random sampling (n=983 plots) within landcover strata from LANDSAT-TM (Franklin et al. 2001). I then statistically modeled peak forage biomass (g/m^2) using the best predictive function of spatial covariates in a GIS. Second, forage growth was spatially modeled from the start (8 May) to the end (15 October) of each growing season in 16-day intervals. In open habitats, forage growth was modeled using the normalized difference vegetation index (NDVI) from MODIS (Huete et al. 2002). In closed habitats, I modeled growth using statistical models of resampled ground plots (n=30). In a GIS, I combined the peak of forage biomass and forage growth models to create 16-day 'maps' of forage availability between 8 May and 15 October at 30 m^2 (Chapter 3). To model overwinter forage decline, I linearly interpolated graminoid-only (assuming forbs were unavailable in winter) biomass between the end and start of the next growing season in a smaller winter-only study area (Appendix 2C). In contrast to predation, which is event driven, survival consequences of forage exposure likely occur over longer temporal scales (Gates and Hudson 1981, Cook 2002). As a result, I calculated an index to cumulative forage exposure for each elk as the running-mean value of exposure to forage using graminoid biomass estimates for each elk reset to 0 each year on 1 June to mimic annual cycles of body condition in wild ungulates (Gates and Hudson 1981, Cook 2002). Note this assumed multi-annual effects of forage biomass exposure were negligible. The value of forage exposure reflected the nearest 16-day value to the date of each observed telemetry location.

Quantifying wolf predation risk exposure

Exposure of elk telemetry locations to wolf predation risk was quantified by combining wolf resource selection functions (RSF, Manly et al. 2002) with their spatial density of use (Chapter 4). First, wolf resource selection was modeled using mixed-effects RSF models where random-effects accomodated pack-level heterogeneity in wolf avoidance of human activity (Chapter 4, Skrondal and Rabe-Hesketh 2004). Because wolves in high-human use areas avoided human activity during the day, predation risk for resident elk that exploited these spatio-temporal refugia was reduced (Chapter 4). I then combined the RSF component of risk with wolf density of use from kernel density estimators and pack size to estimate total predation risk (PRF, Chapter 4).

Elk group size and survival

I used observed or estimated group size as a covariate in the Cox-model (Frair 2005). I obtained visual counts of elk group size from 72% of VHF elk observations, or 4.1 group size counts/elk/month. For missing observations, including all GPS locations, I estimated group size using either: (a) the monthly median group size for each elk, or where observations/month were insufficient ($\leq$2, 35% of all elk-months), or (b) the median group size was assigned for that month and migratory strategy. Differences in group size detection rates between strategies, especially during summer when elk were allopatric, were assumed to be negligible because both strategies used open habitats approximately equally during summer (Chapter 3).

Spatial mortality hazard predictions

The best-supported Cox-model was used to create spatial mortality hazard predictions by applying Eq.1 as a function of spatial covariates in a GIS. Because wolf predation risk and herbaceous forage biomass were time varying covariates, predictions from the Cox-model were specific to a certain time. I made predictions during mid winter (February 2) for the winter model and the peak of the growing season (August 4) for the summer using time-specific forage and predation risk. Moreover, I evaluated risk using the average elk group size in each season.

Reproductive Rates

I determined late-winter elk pregnancy rates for captured elk (n = 141) from 2002-2005 using a pregnancy specific protein B (PSPB) assay in elk blood serum (Sasser 1998) (Biotracking Inc., ID). Mean pregnancy rates are reported by age-class and year for adults. Logistic regression was used to test for the influence of migrant status and a migrant*year interaction, while controlling for the effects of year, age-class, weight, and capture date (Appendix 4). Finally, the frequency of reproductive pauses was estimated using the proportion of consecutive breeding for female elk (Testa 2004a) for whom pregnancy status was determined for $\geq$2 consecutive years. I tested for differences in the frequency of reproductive pauses between strategies and years using chi-square tests.

Elk Calf Survival

I estimated elk calf survival by resighting calves of collared female elk (*sensu* Testa 2004a, Bonefant et al. 2005) with known pregnancy status. I used this method instead of calf:cow ratios' because the latter confound fecundity, age-class structural changes, and calf survival (Gaillard et al. 2000). However, I compared survival from this method to classification data elsewhere (Appendix 1). I resighted calves accompanying collared females during two 'resighting' periods, summer (1 June – 15 August), and winter (1 March – 15 May) in biological years 2003 and 2004. Mean resighting dates were 15 July and 22 March and did not differ between strategies between resighting periods (ANOVA interaction $F_{1,222} = 0.11$, $P = 0.74$), years ($F_{1,222} = 1.82$, $P = 0.17$), or year ($F_{1,222} = 2.13$, $P = 0.11$). Elk were observed for a total of 34 min (SE = 2.6) each per period (24 in summer, 48 in winter) for a total of 147.3 hours. Total summer observation time did not differ between migrants (20 min, SE = 2.9) who were more likely to be observed aerially, and residents (28 min, SE = 3.6). Elk groups were observed from <300m with 45x-60x spotting scopes, or on aerial surveys. Calf presence was noted by observing suckling, grooming, perineal licking, or associated movement (Bonefant et al. 2005). Using repeated observations of known-status female-calf pairs, I estimated the ad hoc resighting probability of detecting a calf, given it was alive, as 0.932 (SE = 0.028, n = 67 known status female-calf pairs). This was similar to Testa (2004b)'s resighting rate of 0.96 for moose, but higher than Bonnefant et al.'s (2005) 0.81 resighting rate for red deer. With 2.1-sightings/resighting period, I had only a 0.004 probability of missing a calf/resighting period. Therefore, I considered calf status (live, dead) as known-fate for survival estimation (Testa 2004b). I combined resighting data with pregnancy status the preceding winter (75% of observed elk had known pregnancy status). Assuming the false-positive rate for pregnancy testing was 0, the pregnancy test was considered a 'resighting' period. Thus, there were three resighting periods and two intervals during which survival was estimated (Fig. 6-1). Late-term abortion rate was assumed to be 0 similar to Nelson and Peek (1982) and Raithel et al. (2006) assuming elk were not under extreme nutritional restriction (Cook 2002). Survival during the interval from pregnancy testing (4 March) to summer (15 July), therefore, reflected neonatal survival, $\phi_{1(\text{neonatal}),}$ from the mean parturition date (June 1) for elk in my study area (Flook 1970, Woods

1991), a 45-day period. Survival during the second interval 15 July to 22 March, a 250 day period, reflected summer and winter survival, $\phi_{2(\text{summer-winter})}$ (Fig. 6-1). Most elk calf mortality occurs during the neonatal period (Smith and Anderson 1996, Singer et al. 1997, Barber et al. 2005). I therefore assumed survival for the remainder of the calendar year, from 22 March to 31 May was equal to ϕ_2 to estimate annual survival rates of calves ϕ_{annual}.

Elk calf survival was modeled using program MARK (White and Burnham 1999), and included different seasonal survival rates for ϕ_1 and ϕ_2 above, and group-level covariates for migrant status and year (2003, 2004). Calves of collared females that were not observed in the summer were censored because interval specific rates could not be calculated (Fig. 6-1, White and Garrot 1990). The top model was selected using AICc (Burnham and Anderson 1998) from a competing set of all possible candidate models including models for constant winter survival between years and strategies based on the shared winter range. Goodness of fit testing for known fate models was uncertain, therefore, I used a bootstrap GOF test to approximate $\hat{c}$ to correct for overdispersion if necessary (White and Burnham 1999). Monthly survival rates were calculated for each survival interval to facilitate comparison. For calculation of monthly and annual survival rates, I used the delta method to derive variance estimates.

Fitness Balancing between Migrant and Residents

I constructed elk matrix models to estimate population growth rates of migratory and resident elk. To evaluate fitness balancing, I estimated the rate of change of the M:R ratio between migrants and residents using the ratio of migrant to resident population growth rates. I modeled elk life history in 5-age classes; calf (<1 year-old), yearling (1-2 years), prime-age adult (2-10), old-age adult (10-15), and senescent (>15) closely following Raithel et al. (2006). I divided adults into prime-age and old-age to account for survival declines prior to senescence (Gaillard et al. 2000, Flook 1970). I modeled elk population growth rate using these female elk age-classes in a pre-birth pulse age-structured Leslie projection matrix (Caswell 2001). Pre-birth censuses best describe ungulate populations where population counts occur during late winter prior to birth. Reproduction occurs at ages $\geq$ 2 years. Calf survival was assumed to be constant between sexes, and sex ratio at birth was assumed 50:50. In pre-birth pulse models, the top-row of the Leslie matrix is the product of fecundity and calf survival. Fecundity is the product of the number of female calves born, intrauterine survival, and pregnancy rate. Elk were assumed to bear one young (Raedeke et al. 2002) and because pregnancy was estimated on 8 March, late-term intrauterine survival was also assumed to be 1 (Raithel et al. 2006, Nelson and Peek 1982). Thus, fecundity was simply the half the pregnancy rate. For full matrix details see Appendix 4.

I used data from this study for migrant and resident age–specific vital rates where possible, augmented where necessary from a comprehensive recent review of over 40 elk studies by Raithel et al. (2005, 2006). Pregnancy rates from this study were used to estimate fecundity (F) for F_{yly} and $F_{\text{prime-age}}$, where only $F_{\text{prime-age}}$ differed between migrant strategies. $F_{\text{old-age}}$ and $F_{\text{senescent}}$ were assumed to be the same decline in pregnancy from $F_{\text{prime-age}}$ to $F_{\text{old-age}}$ and $F_{\text{senescent}}$ as Raithel et al. (2006). Estimates for resident and migrant mean annual ϕ_{calf} (calf survival) came from this study. Like many studies (reviewed by Gaillard et al. 2000), ϕ_{adult} was only estimated for all elk >2 years old, yet age-structure has important effects on ungulate population dynamics (Gaillard et al. 2000). Therefore, I used Raithel et al.'s (2006) life-table approach to decompose the pooled ϕ_{adult} into ϕ_{yly}, $\phi_{prime\text{-}age}$, $\phi_{old\text{-}age}$, and $\phi_{senescent}$ age-class survival rates based on the age distribution (13% yearlings, 72% prime-age, 10% old-age, and 5% senescent) and survival of elk from Yellowstone National Park (Houston 1982). Age-class survival rates were calculated proportionately from Houston (1982) such that when weighted by the age-distribution was equal to the mean annual survival rate for both strategies (Raithel et al. 2006).

I used the analytic solution of the resident and migrant matrices to estimate the deterministic population growth rate, λ, and elasticity following Caswell (2000). Uncertainty in analytic λ was estimated using the series or delta approximation (Caswell 2001: p 300). Analytic elasticity is defined as the proportional change in λ resulting from infinitesimally small, one-at-a-time changes in a matrix element while holding effects of all other elements constant (Caswell 2001). Recent studies have noted, however, that vital rates with the highest elasticity hardly vary, such as adult female survival in large herbivores (Gaillard and Yoccoz 2003, Coulson et al. 2005). By not including information about variability in vital rates, analytic sensitivity analysis often fails to identify demographic drivers (Wisdom et al. 2000). Thus, life-stage simulation analysis (LSA) was used to explore the effects of vital rate variation in population growth rate and elasticity (Wisdom et al. 2000). LSA simulates replicate matrix models using vital rates drawn at random from a mean and process variance (Wisdom et al. 2000). Process variance is estimated using variance components decomposition from time-series or across point estimates (White 2000). I used mean vital rates for elk in my study as defined above. However, given the short-time span of this study (3-years), I did not estimate process variance, but used the *within-study* process variance estimates ($\hat{\hat{\sigma}}^2_{within}$)

from Raithel's (2005) comprehensive review. Given these vital rates and process variance estimates, 1,000 replicate matrices were simulated from the observed distribution for each vital rate using the limitsens.m MATLAB code from Morris and Doak (2002) modified for elk by Raithel et al. (2006). In the absence of quantitative data for elk, the potential effect of covariance between vital rates was ignored (Coulson et al. 2005).

For comparison to estimates of λ from matrix models during 2002-2004, I estimated λ_{M-N} and λ_{R-N} from the total population counts (N) of elk from Chapter 2, Table 2-2. Recall the M:R ratio was calculated in Chapter 2 using the number of residents N_R observed in summer t, and the number of migrants, N_M, was calculated based on the population count the *following* winter t+1. Hence in Table 2-2, Chapter 2, the unreported elk counts for 2005 (biological year 2004/2005) are required to estimate $N_{M-2004.}$ Counts were obtained from ABFW aerial surveys during 2005 (ABFW, unpublished data).

RESULTS

Elk Capture and Monitoring

Of the 120 collared elk used in the survival analysis, 53 (45%) were residents and 65 (55%) were migrants. Each elk was monitored for a median 1.4 years, or 550 days in a median 46.5 six-day intervals. I monitored elk for 150 migratory seasons in total, and two elk followed for at least two full years switched between migratory strategies a total of three times (one switched each year of the study) for an ad-hoc switching rate of 2.0%/elk/year. Switching occurred both ways, from migrant to resident (n=1) and vice versa n=2). Adult migrant and resident elk did not differ in either body mass or condition (Table 6-1). However, female young of the year body mass was higher for migrants

(117.8 kg, n = 8) than residents (97.3 kg, n = 11) (unequal variance t-test $t_{16,\,0.05} = -4.068$, $P < 0.0001$).

Adult Female Survival

A total of 39 mortalities occurred during the period from 2 February 2002 to 30 November 2004 (18 migrant, 21 resident, Fig. 6-2). Wolves were the largest source of mortality (43%), followed by human harvest (26%), grizzly bears (19%), and other sources (11%) of mortality including coyote, cougar, and disease/starvation. Human harvest was comprised of 18% bow hunting, 18% rifle, and 18% poaching, and 46% by treaty First Nations. Annual timing of mortality peaked in June, driven by grizzly bear predation, and during September and October resulting from human hunting. A secondary peak in December was caused by First Nations harvest (Fig. 6-2). Wolf-caused mortality occurred year-round (Fig. 6-2). Mortality causes differed between migrant and residents (χ^2-test = 20.82, $P = 0.0001$). Although there were three times more migrants killed by grizzly bears than were residents, the significant difference was driven by higher human harvest of residents (Fig. 6-2; post-hoc test $P < 0.01$, Haberman 1973). Wolf-caused deaths were high, but relatively similar between residents and migrants. More deaths of resident than migrant elk were attributed to First Nations peoples (4 vs. 1), rifle harvest (2 vs. 0), bow hunting (4 vs. 0) and poaching (1 vs. 1), with most of the resident elk (7/9) harvested during 2004.

Survival rates

Average survival rates across the study for residents were 0.840 (SE = 0.032) and 0.862 (SE = 0.035) for migrants, but did not statistically differ (log-rank χ^2-test, d.f. = 1, $P = 0.31$). However, resident survival rates varied between years and were significantly higher than migrants in 2002 (log-rank χ^2-test, d.f. = 1, $P = 0.03$) but lower than migrants in 2003 (log-rank χ^2-test, d.f. = 1, $P = 0.05$)(Table 6-2). Cause-specific mortality rates illustrated that migrants had higher wolf and grizzly mortality, especially, while residents had higher human mortality (Table 6-3).

Survival risk factors

Survival of migrant elk did not meet proportional hazards assumptions (e.g., the cumulative hazards crossed) because baseline hazard rates differed between migratory strategies (Fig. 6-3). I therefore stratified survival models by resident and migrant strategies. Including season (winter, summer) did not improve any models as either covariates or strata. The top model was selected with reasonable certainty (ΔAICc = 2.5) between the first and second ranked models. The top model met all proportional hazards assumptions, indicated by the Schoenfeld residuals goodness of fit test ($\chi^2 = 1.72$, $P = 0.787$), and linear Cox-Snell partial residual plots. The top model also showed a reasonable fit to the data (LR $\chi^2 = 9.82$, $P < 0.043$) and reasonable predictive accuracy between the ranked daily hazard vs. the frequency of deaths (Spearman's rho = 0.852, $P = 0.0015$, n = 10 bins). Coefficients from the top model are presented as hazard ratios (Riggs and Pollock 1992, the natural logarithms of the β's in Eq.1), where a hazard ratio < and > 1 implies reduced or increased odds of death, respectively. The same covariates occurred in the top model for both migratory strategies; no covariates were retained in the top model were specific to only one migration strategy.

Elk mortality hazard decreased (e.g., <1) as the annual running mean exposure to herbaceous biomass increased. Hazard also paradoxically declined with increasing wolf predation risk (Table 6-4). However, this apparent paradox was because of the odds >1 for the F*P interaction (Table 6-4), indicating increased hazard in areas of both high forage and predation risk (e.g., Fig. 6-4). Mortality hazard was constant up to elk group sizes of ~75, after which it declined exponentially (Table 6-3, Fig. 6-5). Group size differences were most pronounced in summer (June-August) when resident elk lived in an average group size of 93.1, where as migrants lived in much smaller groups, averaging 31.2 (Fig. 6-5). These seasonal group size differences alone translated to migrants having ~20% higher hazard. Despite reasonable information theoretic support for this model, however, coefficient estimates were not significant, with P-values between 0.06 and 0.15 (Table 6-3)

Spatial mortality hazard predictions

During winter, mortality hazard was spatially concentrated on the YHT winter range and Dogrib burn just east of YHT (Fig. 6-6). At a finer-scale, predation risk increased along a gradient from closed conifer to open grassland habitats. During summer, mortality hazard was much more diffuse, with scattered patches of high mortality hazard in grasslands and burns especially near wolf denning sites (Chapter 4) because of the interaction between predation and forage (Fig. 6-4, 6-6).

Pregnancy Rates

Pregnancy rates varied from 0.66 to 0.98 during 2002-2005 (Table 6-4). Yearling pregnancy was low at 0.167 (Table 6-4). Overall, migrants had higher pregnancy rates (Logistic regression $\beta_{migrant} = +2.90$, SE = 1.21, $P = 0.001$, Appendix 5) than residents, except during 2003 (interaction $\beta_{migrant*2003} = -3.43$, SE = 1.82, $P = 0.001$). Of 158 females, I determined consecutive pregnancies for 23 elk for two-years and 3 elk for three-years. Excluding one female elk that was barren in both years, only 62% (n = 16) bred consecutively each year. Migrants had higher prevalence of consecutive breeding (68%) compared to residents (57%), but this difference was not significant ($\chi^2 = 5.1$, $P = 0.21$).

Elk Calf Survival

Survival of 79 calves (33 of resident cows, 46 of migrant cows) from 65 individual collared females (30 residents, 35 migrants) were monitored during 2002 and 2003 from pregnancy testing on March 8 to March 22 the following year (See Table 6-6 for annual sample sizes). Because $\hat{c}$ = 1.504 was <1 in the overall bootstrap GOF test, I corrected for overdispersion by inflating variances using quasi-likelihood methods (White and Burnham 1999). In the top model (AIC *weight,* $w = 0.53$), survival varied between neonatal and summer-winter intervals but was constant between strategies and years. The second ranked model (AIC $w = 0.26$) indicated survival was different between intervals and also strategies during the neonatal interval, but not the summer–winter interval. The third ranked model included yearly differences in survival rates but had weak support (AIC $w = 0.10$, Appendix 5). Given model selection uncertainty (Appendix 5), I used model averaging for parameter estimation (Burnham and Anderson 1998) and reported the average calf survival for strategies and years in both intervals, as well as the overall average. Overall neonatal interval survival, $\phi_{1(\text{neonatal})}$, was 0.696 over the first six weeks of life, and summer-winter survival, $\phi_{2(\text{summer-winter})}$, was 0.266 for the remainder of the year, resulting in an average annual calf survival rate of 0.185, assuming survival after March 22 equaled $\phi_{2(\text{summer-winter})}$. Migrant $\phi_{1(\text{neonatal})}$ was 0.615, lower than neonatal survival for residents, 0.697, but not significantly so because of the large SE's (Table 6-6). Summer–winter survival, $\phi_{2(\text{summer-winter})}$ was similar for both migrants and residents

(0.266 vs. 0.265). Combined, annual calf survival rates for migrants, 0.163, were lower than residents, 0.185, though the wide standard errors for both indicate calf survival rates were not significantly different. Survival during both intervals was higher in 2004, resulting in annual survival rates of 0.148 and 0.226 in 2003 and 2004, respectively, though again, wide SE's indicated annual differences which were not statistically significant (Table 6-6). In all models, the calculated monthly survival rate was higher after the neonatal period (Table 6-5).

Fitness Balancing Between Migrant And Residents

Vital rates and estimates of process variance used in matrix-models are summarized in Table 6-7. Analytic population growth rates estimated from the mean matrix (lambda, λ) of migrants and residents were $\lambda_M = 0.878$ (SE = 0.028) and $\lambda_R = 0.901$ (SE = 0.027), with confidence intervals overlapping each other (migrants 95% CI 0.822 to 0.933, residents 0.848 to 0.954, Table 6-9), but not $\lambda = 1$. As a result, the number of either strategy declined during this study at a rate of 10-12%. The proportion of residents in the population increased at a rate of λ_R/λ_M = 2.4 %/annum, though given the wide confidence intervals of λ_R and λ_M, confidence in the rate of change of the proportion of residents was similarly low. Analytic elasticity of different vital rates did not differ between resident and migrant elk, with the highest elasticity for prime age-adult (0.618, 0.621), followed by calf and yearling survival (0.124 for all), old age survival (0.105, 0.104), and prime-aged pregnancy (0.08 for both)(Table 6-8); other vital rates elasticities were <0.05 (Table 6-8).

Accounting for uncertainty in vital rates using LSA, migrant and resident estimates of λ were $\lambda_M = 0.866$ and $\lambda_R = 0.894$, similar to analytic estimates (Table 6-9), with similar overlapping confidence intervals. Despite statistical overlap, the ratio of λ_R/λ_M from LSA suggested that resident proportion of the population increased by 3.2%. Accounting for within-study process variance ($\hat{\hat{\sigma}}^2_{within}$) in vital rates dramatically changed the relative importance of vital rates to λ compared to analytic elasticity (Table 6-8). In 1,000 random matrix model simulations, the coefficient of determination (r^2) between λ and vital rates was the highest for calf survival for migrants and residents, $r^2 = 0.834$ and 0.825, followed distantly by prime-age adult survival of $r^2 = 0.073$ and 0.05 (Fig. 6-7). All other vital rate r^2 from LSA were <0.05 (Table 6-8), indicated that these two rates accounted for ~90% of the variance in λ. The maximum proportional change observed in λ from changing calf and adult survival rates was 0.3 and 0.12 for both strategies, indicating calf survival had a 2.5-fold greater maximum effect on λ.

Finally, from population counts for biological years 2002 and 2004, the number of migrants, N_{M-N}, declined from 592 to 473, and N_{R-N} declined from 324 to 267 (Chapter 2, AB-SRD, unpubl. data), which translated to average annual $\lambda_{N-M} = 0.89$ and λ_{N-R} 0.91, very similar to the vital rate estimates. The ratio of $\lambda_{N-R} / \lambda_{N-M}$ from population counts was 1.3%, confirming a relative increase in the proportion of residents.

DISCUSSION

Migrant and resident elk exhibited demographic differences that suggested residents may be demographically outperforming migrants in this population. Adult female survival rates were slightly higher for resident elk than migrants, similar to partially migratory populations of moose in Sweden (Andersen 1990), passerine songbirds in Europe (Perez-Tris and Telleria et al. 2002, Berthold 2002, Adriansen and

Dhondt et al. 1990), and giant tortoises in the Pacific (Swingland and Lessels 1979), confirming a general trend across partially migratory taxa. Resident calf survival was also slightly higher than migrant calf survival. Higher adult and juvenile survival for residents appears in contrast, however, to other partially migratory populations. Resident moose in Sweden, for example, had higher hunting related mortality, but higher calf survival compensated (Andersen 1990). Likewise, resident giant tortoises had higher adult survival, yet lower juvenile survival rates. Yet partially migratory songbirds were similar to elk whereby resident European robins had higher adult and juvenile survival rates (Adriensen and Dhondt 1990). Higher adult and juvenile survival of residents lead to higher growth rates, which would result in the proportion of migrants in the population declining.

Regardless of the changes in relative proportions of migrants and residents, both strategies declined rapidly at an annual rate of ~10-12% over 2003-2004. This was because the vital rates reported for both migratory strategies in this study were much lower than vital rates in other elk populations (Raithel et al. 2006). Raithel et al. (2006) reviewed over 40 studies of elk demography where the average λ was 1.0, and found average adult, calf, and prime-age pregnancy rates were 0.873, 0.354, and 0.928, respectively; all higher than the vital rates observed in this study for either migrants or residents (Table 6-6). While both populations were declining in this study, migrants were declining slightly faster, increasing the proportion of residents in the population. However, the demographic differences observed between migrant and resident vital rates were not statistically significant in this study. Despite these relatively small demographic differences, I interpret them as biologically significant for two main reasons. First, the ratio of $\lambda_M:\lambda_R$ was consistent with the declining M:R ratio observed from 1977 to the present of 1.5% per year (Chapter 2). Second, and perhaps most compelling, the rate of decline from vital rates matched the rates of decline from population counts (N) of residents and migrants (Chapter 2). Therefore, despite weak statistical support for differences in λ between strategies, estimates appeared biologically realistic, suggesting that low-precision estimates may indeed be useful (Mayer et al. 2002).

Previous work in this population suggested the relatively higher fitness of residents arose from differences in resource selection. While migrants avoided wolf predation risk at large spatial scales, they had higher cause-specific mortality from wolves and especially, relative to residents. Migrant mortality peaked in June, consistent with the observation that migration, which also peaks in June, entailed a direct cost (Chapter 5). By avoiding predation risk at large scales, regardless of overall mortality, migrants had 4-5% higher forage digestibility through the summer (Chapter 3). This forage benefit manifested in higher pregnancy rates and higher female calf weight. In contrast, the resident strategy to avoid predation by staying close to human activity reduced wolf and grizzly predation at the expense of higher human-caused mortality. Residents also entailed direct cost to foraging by avoiding increasing wolf predation risk, by avoiding areas with the highest forage quality (Chapter 3, 5). This resulted in lower fecal nitrogen (Chapter 3), pregnancy rates, and calf weights for resident elk, confirming the costs of risk avoidance were real from a nutritional perspective (Cook 2002).

The superior demographic performance of residents, despite this nutritional advantage held by migrants, suggests top down effects were more important. With the extensive prescribed fires on migrant summer ranges (Chapter 3) and their beneficial effect on elk forage (Sachro et al. 2005), I expected larger bottom-up effects on migrant elk demography. Similarly, in Chapter 2 and White et al. 2005, time-series analyses indicate that in the presence of wolf predation, the effects of fire on elk population growth rate is negative, not positive. Further implicating the importance of top-down effects is that in this study I ignored grizzly bear predation risk, given logistical constraints. Migrant exposure to both grizzly and wolf predation risk was certainly higher than residents because grizzly bears also avoid human activity (Gibeau et al. 2002), are attracted to burned areas for foraging (Hamer 1996, 1999), and the YHT is a grizzly mortality sink (Nielsen et al. 2004). These three factors likely explain the three-fold higher grizzly bear mortality of migrants. Future research will be able to use regional grizzly bear resource selection modeling (e.g. Nielsen et al. 2003) to test whether by migrating and selecting burned areas, elk are avoiding wolf predation only to "move from the frying pan into the fire."

Residents also benefited from living in 2-3 times larger group sizes than migrants, reducing mortality hazard by an additional 20%. The exponential benefits of group size suggest predation by wolves could cause depensatory predation above a critical elk group size-density threshold of about 75-100 elk. Because residents occur in a few large herds during summer, wolf encounters with residents would quickly saturate (Huggard 1993) and predation rates could become inversely density dependent as elk density, and thus group size, increases (e.g., Hebblewhite and Pletscher 2002). Grouping may allow residents to 'escape' predation, suggesting the existence of two migratory stable states for the ESSt proportion of residents. Critically, large group sizes were only possible because of the high forage biomass at the YHT that contributed to reduced mortality hazard. Thus, the demographic advantage of residents arises because of a complex interaction between forage, predation risk, and human activity. Resident selection for reduced predation risk because of human activity combined with the benefits of living in larger group sizes. And the co-occurrence of high human activity with the high forage biomass grasslands of the YHT made this possible. Without these interactions, forage biomass would have to be much greater, or predation risk much reduced, to achieve the same benefits for residents.

The slightly higher frequency of reproductive pauses in resident elk suggests demographic trade-offs may have been occuring. The imbalance between strategies suggested either poorer forage quality and/or higher risk-forage ratio's for residents relative to migrants (Pulliam 1983, Testa 2004a,b). However, the high overall frequency of reproductive pauses (~40%) suggests two different mechanisms may also be at work. Reproductive pauses could have been frequent either because 1) elk density was near nutritional carrying capacity (Cook 2002), or 2) females with calves experienced higher predation pressure and made life-history trade-offs between survival and reproduction (Testa 2004a,b). The winter population during this study was ~900 elk (Table 2-2, Chapter 2), near the long-term nutritional carrying capacity (~1,200, reviewed in Chapter 2). However, the first 3-years of the study were amongst the driest summers in 30-years (Chapter 2, 3), suggesting drought conditions may have influenced the frequency of reproductive pauses. Pregnancy rates were the lowest in these three dry years, but increased to >0.95 in the wettest year of the study, 2005 (Table 6-4), confirming nutritional explanations. However, the peak of grizzly bear predation (33% of all grizzly predation) in June indicates trade-offs between adult female survival and reproduction may also be occurring similar to moose (Testa 2004a). Future research on elk demography will be required to tease apart the relative roles of forage or predation on trade-offs between survival and reproduction.

While wolf mortality was the leading cause of mortality, human hunting was five times higher for residents. Curiously, this occurred even during winter when residents and migrants were together on the YHT. This suggests either spatial partitioning may be occurring, or that residents had higher vulnerability to hunting, perhaps because of habituation to human activity (Thompson and Henderson 1998). The high levels of human hunting mortality of residents observed in this study did not reflect mortality trends over the past 25-year because the legal female harvest only occurred from 1999-2003. The female harvest opened in early September, and perhaps because this was prior to the mean fall migration date (Chapter 2), legal-harvest appeared to select residents (no migrants were legally harvested). Assuming no legal hunter-caused harvest during both years (but still First Nations harvest) and no changes in other vital rates, resident λ_R = 0.95, an even greater increase relative to migrants, which were not legally harvested. With no legal-harvest and the highest calf survival rates observed in 2004, λ_R = 1.02. Because the high First Nations harvest in 2003 is typically observed only once every 5 years or so (Appendix 1), assuming no human caused mortality on residents would have increased λ_R to 1.01, other vital rates were constant.

These relatively modest changes to λ given relatively large changes in legal-harvest reveal the key role that calf survival plays in determining elk population growth rate (Raithel et al. 2006). Population growth rates of both strategies were equally sensitive to variation in calf survival in my LSA. By using process variance estimates from Raithel et al. (2006) instead of from my own study, I may have overestimated the importance of calf survival to λ. For example, assuming the proportion of total variance in calf and adult survival that was process variance (88, 54%) from Raithel et al. (2006) applied to my study, the ratio of variance in calf to adult survival was 4.0 and 4.5 for migrants and residents (from SE's in Table 6-s 1, 5, 6), less than the 10 and 12.5 fold difference of Raithel et al. (2006). Regardless, this still emphasizes the importance of calf survival to elk λ. As a final caveat, I ignored covariance between vital rates. Yet covariation between vital rates can explain one-third to one-half the variance in λ (Coulson et al. 2005), which would de-emphasize the importance of calf survival in my example. Interestingly, however, Coulson et al. (2005)'s study had positive covariance between adult and calf survival in two ungulate populations with low predation pressure. The trade-off between adult female and calf survival revealed by Testa (2004a) in moose may lead to negative covariance between vital rates in predator-regulated systems, and the effects of this certainly warrants more investigation.

Calf survival was clearly important for elk λ, which begs the question of what calf survival rates would be required to have observed the growth from 30 resident elk in 1980 to ~350 in 25 years. While adult and calf survival estimates are unavailable for the 1977-1980 period (Morgantini 1988), wolf populations were recolonizing and there was no legal female harvest. Morgantini (1988) also reported calf:female ratios of 0.33, approximately a 0.40 calf survival rate given adjustments for pregnancy rates (Bonefant et al. 2005, Appendix 1). Therefore, I evaluated the effect on λ of 50% less wolf mortality, no legal hunting, and calf survival of 0.40. Under this scenario, λ of both strategies would have been 1.08 in 1980, which if constant, would have resulted in 230 residents and ~2,388 migrants by 2005 (see Chapter 2, Table 6-2). The population peaked close to 2,200 elk in the early 1990's, and has since been declining or stable concomitant with a declining M:R ratio (Chapter 2). Clearly density dependence of some form, whether by predation or intra-specific competition or both, reduced elk λ since this population peak. Given the high predation mortality reported in this study, I suggest it is density-dependent wolf predation (and grizzly bear predation) that has regulated λ of both strategies, but especially for migrants (e.g., Messier 1994). Wolf predation in the nearby Bow Valley of BNP in limited elk populations to ~50% of areas without wolves in concert with winter severity (Hebblewhite 2005). While there is some uncertainty over whether wolves can regulate elk populations (Vucetich et al. 2005, Eberhardt et al. 2003), broad support for regulation on theoretical and empirical grounds (Messier 1994, Dale et al. 1994), especially in combination with grizzly predation (Orians et al. 1997) make it very likely that predators will regulate elk to low densities. Clearly, future research is needed on what conditions density-dependent wolf predation on elk is expected, and how predator-regulation may differ between migratory strategies.

One crucial assumption to the strict demographic interpretation of changes in the M:R ratio is that strategies are fixed for the life-time of individual elk. While elk display high fidelity to a migratory strategy (Van Dyke et al. 1979), elk are behaviourally plastic (Geist 2002). Indeed, low levels of switching, 2%/year, were observed between strategies during the 3-year study. No directional bias in switching was observed, for example, more elk switching from migrant to resident status. However, our 3-year study was of insufficient duration to examine lifetime behavioural strategies used to maximize reproductive success (Clutton-Brock et al. 1982, Geist 2002). Therefore, I caution my assumption of a fixed-strategy in this population. A slow behavioural switch of even

1%/year from migrant to resident, over the duration of the migrant decline in this population (1977-2005), could certainly potentially play as important a role as demographic differences. If switching occured, this suggests the potential for a conditional mixed ESS may exist in this elk population, where condition is an external condition like predation risk, not an internal condition like body weight as is commonly observed (i.e., Adriensen and Dhondt 1990, Lundberg 1988). Regardless, the strict demographic interpretation assuming fixed-strategies is certainly useful for management. This is because management agencies make decisions to affect populations, not individuals. If residents have increased as a result of a combination of fixed-demographic differences and conditional switching between strategies, the management interpretations are similar: resident elk populations increased. However, management responses may differ dependent on the inferred behavioural flexibility of elk. For example, if restoring migratory behaviour is only possible demographically, and not behaviourally, aversive conditioning will fail to persuade resident elk to 'switch' to a migratory state. Unfortuneately, even with a large study such as this on demography, long-term monitoring is required to address these behavioural questions in more detail.

Despite the benefits of higher forage quality and reduced wolf predation risk experienced by migrants in this system, resident fitness was relatively higher than migrants, because of reduced predation due to human activity. The fitness balance in favor of residents is consistent with the long-term decline in M:R ratio. Simple population modeling suggests that relatively recent increases in human harvest of residents may explain the recent declines in resident populations. Migrants on the other hand, while they benefit from reduced predation risk on summer ranges, faced higher relative hazard there because of their smaller relative herd sizes, and elevated predation risk from both wolves and potentially grizzly bears, leading to higher mortality. Whether this suggests there is no ESSt for a stable proportion of migrants, p*, in the population is unknown. While the proportion of migrants has been declining for some time, it seems unlikely that the density-dependent mechanisms regulating the number of migrants and residents suggest complete fixation at 100% residents. Instead, it seems likely that p* will gradually reach stability at some low number, maintained by environmental stochasticity, which allows a few migrants to persist. In support of this interpretation, following wolf recolonization of the Bow Valley, combined with similar human influences, the migrant to resident ratio declined to 0.15 (Woods 1991; McKenzie 2001). Given the high predation on migrants and potential for predator regulation, it is quite difficult to envision abundant migratory elk coexisting with the levels of wolf and grizzly bear predation observed here. Adding historic human predation by First Nations, as part of the long-term range of variability, makes it even more difficult. In fact, archaeological and historical studies paint a similar picture as this ecological investigation, suggesting historically low and scattered migratory elk populations in montane systems that were dominated by bison and bighorn sheep in the ungulate communities (White et al. 2001, Kay et al. 2000, White et al. 1998). Given the relatively rapid shift from an almost pure migrant strategy to one that is mixed over a 20-year period, and the low proportion of migrant elk in the nearby Bow valley over a similar time-frame, I suggest the proportion of migrants in this system has two evolutionary stable states. Either near fixation for migrants or resident strategies, but no intermediate stable mixed proportion, and a transition triggered by wolf recolonization.

Table 6-1. Average differences between adult female elk in late winter body weight (KG), condition index scores, and between YOY female body weights, averaged across 2002-2005, YHT elk population, BNP.

	Migrant		Resident		P-value
Adult female weight (KG) †	232.9	45	231.4	46	0.5
Adult female body condition‡	3.11	66	3.41	66	0.44
YOY female weight (KG) †	117.9	8	97.3	11	0.0001

Notes: adult female body weight and condition compared using an ANOVA by year and migrant status, and their interactions. There were no significant effects, so only the P-value for migrant status is reported here; see Appendix 5 for more details.

† - Mid winter body weight measured at a mean date of capture of March 4 each year; note that body mass did not significantly vary across the range of capture dates.

‡ - Body condition index was an ordinal scale from 1 (starving) to 6 (excellent) following Cook et al. (2002).

Table 6-2. Kaplan-Meier seasonal and annual adult female survival estimates ϕ, February 2002 to October 2004, YHT elk population, BNP.

			Resident			Migrant	
Season	Bioyear	n-risk	Survival ϕ	S.E.	n-risk	Survival ϕ	S.E.
Winter	2001††	19	0.956†	0.025	20	0.956†	0.025
Annual	2002	33	0.944^{a}	0.054	34	0.846^{b}	0.086
Annual	2003	42	0.762^{a}	0.065	62	0.835^{b}	0.048
Summer	2004††	36	0.890^{a}	0.067	48	0.875^{a}	0.060
Summer	Mean	51	0.887^{a}	0.062	64	0.868^{a}	0.064
Winter	Mean	49	0.934^{a}	0.039	62	0.955^{a}	0.042
Annual	Mean	53	0.862^{a}	0.032	68	0.840^{a}	0.035

Notes: n-risk is the number of elk at risk during the season/year. Survival rates marked with different letters (a,b) within a row are significantly different (log-rank χ^2-test (1) $P<0.05$). Summer is 184 days, winter 181 or 182 in 2003 (leap-year).

† - One survival rate was estimated for both strategies because of small sample size of mortalities.

†† - Estimated assuming that survival in the unsampled portion of these two seasons was equal to the sampled portions.

Table 6-3. Average annual cause-specific mortality rates of migrant and resident elk during 2002-2004, eastern slopes of BNP.

% Mort	Migrant	SE	Resident	SE
Wolf	0.076	0.010	0.053	0.009
Harvest	0.015	0.004	0.059	0.010
Grizzly	0.046	0.007	0.013	0.004
Other	0.023	0.005	0.013	0.004

Notes: SE's calculated via the delta approximation. Harvest includes legal bow and rifle, poaching, and treaty First Nations harvest. Other includes cougar, coyote, and disease.

Table 6-4. Risk factors from the top Cox-proportional hazards model influencing mortality of resident and migrant elk in the eastern slopes of BNP, 2002-2004. Effects are reported as hazard ratio's (β*X*) and are directly interpretable as odds ratios, with associated SE and P-values.

Risk factor	Hazard ratio Ln($e^{\beta X}$)	SE	P
Herbaceous biomass (g/m^2, annual running mean)	0.957	0.023	0.074
Wolf predation risk (pack-level, unitless)	0.077	0.178	0.11
Forage * predation risk interaction	1.149	0.090	0.077
Group size	0.998	0.002	0.15

Table 6-5. Pregnancy rates for migrant and resident elk in adult, yearling, and subadult age classes. Rates determined from PRS-B testing during late winter (Mar 4) 2002-2005, YHT elk population.

	Resident			Migrant		
Adult Pregnancy Rate	(%)	N	SE	(%)	N	SE
2002	0.67	15	0.031	0.75	16	0.027
2003	0.94	16	0.015	0.88	25	0.013
2004	0.71	14	0.032	0.96	25	0.008
2005	0.95	18	0.012	0.98	12	0.012
Mean adult	0.83†	63	0.011	0.90†	78	0.007
Pooled across strategies						
Yearlings	0.17	6	0.010			
Subadults	0.75	11	0.020			

Notes: yearlings age <1.5, subadults <2.5, adults≥3.

† -The logistic model for pregnancy showed migrant pregnancy rates were higher than residents.

Table 6-6. Unconditional survival estimates averaged the top survival models including strategy, season, and yearly effects, using Akaike weights for migrant (n= 33) and resident (n= 46) elk calves during the 2003 and 2004 biological years YHT elk population, BNP, Alberta.

		ϕ	SE‡	Monthly††	SE‡
Resident					
	Neonatal§	0.697	0.064	0.782	0.055
	Sum-Win¶	0.266	0.055	0.853	0.061
	Annual†	0.185	0.067	---	---
Migrant					
	Neonatal§	0.615	0.078	0.719	0.062
	Sum-Win¶	0.265	0.054	0.853	0.071
	Annual†	0.163	0.082	---	---
2003					
	Neonatal§	0.644	0.067	0.741	0.051
	Sum-Win¶	0.23	0.077	0.838	0.061
	Annual†	0.148	0.068	---	---
2004					
	Neonatal§	0.748	0.083	0.821	0.072
	Sum-Win¶	0.302	0.11	0.866	0.094
	Annual†	0.226	0.093	---	---
Overall					
	Neonatal§	0.696	0.054	0.782	0.056
	Sum-Win¶	0.266	0.045	0.853	0.046
	Annual†	0.185	0.049	---	---

Notes: βs for neonatal and sum-win interval derived from models. SE's for interval βs from the model. SE's for annual/monthly rates via the delta method.

†† - Provided to facilitate comparison between intervals, calculated from daily rates/ interval.

§ - Neonatal interval average 45 days, Jun 1 to July 15.

¶ - Sum-Win survival is the estimate for 250 days, July 15 to March 22, extrapolated to the last 70 un-sampled days is the same using $\phi^{(320/250)}$.

† - Annual survival is the product of the interval specific estimates. See text for further details.

Table 6-7. Migrant and resident female elk vital rates and within-population process variance ($\hat{\sigma}^2_{within}$) estimates used in matrix population modeling.

Vital rate	Migrants Parameter Estimate	Migrants $\hat{\sigma}^2_{within}$	Residents Parameter Estimate	Residents $\hat{\sigma}^2_{within}$
Calf survival (ϕ)†	0.163	0.025	0.185	0.02
Yearling ϕ ‡	0.849	0.0025	0.865	0.0025
Prime-age ϕ ‡	0.848	0.002	0.875	0.002
Old-age ϕ ‡	0.830	0.002	0.845	0.002
Senescent ϕ ‡	0.695	0.0035	0.707	0.0035
Yearling pregnancy†	0.170	0.0085	0.170	0.0085
Prime-age pregnancy††	0.900	0.01	0.830	0.01
Old-age pregnancy ††	0.836	0.0017	0.766	0.0017
Senescent pregnancy ††	0.530	0.0044	0.530	0.0044

Notes: process variance is the average within population process variance reported from a review of >40 elk population studies in Raithel et al. (2006). Yearlings are age 1-2, Prime age adults 3-10, old-age adults 11-14, and senescent adults ages 15+.

† - Direct estimates from this study.

‡ - Estimated based on overall adult female ϕ from this study decomposed into the different adult female age-class survival rates based on (Houston 1982) following (Raithel et al. 2006).

†† - Prime-age and yearling pregnancy rates were estimated from this study, and old-age and senescent rates were estimated based on prime-age following (Raithel et al. 2006).

§ - Process variance in calf survival was higher for migrants similar to SE’s from Table 5.

Table 6-8. Comparison of the results of sensitivity analyses using analytical elasticity for mean vital rates and life-stage-simulation analysis (LSA) r^2 values between lambda and the vital rate for 500 random matrix model replicates.

	Migrant		Migrant	
Vital Rate	Elasticity	LSA r^2	Elasticity	LSA r^2
Calf survival	0.124	0.834	0.124	0.825
Yearling	0.124	0.006	0.124	0.002
Prime-age	0.618	0.0728	0.621	0.0499
Old-age	0.105	0.011	0.104	0.02
Senescent	0.03	0.016	0.027	0.009
Yly Preg	0.003	0.0034	0.003	0.0002
PA Preg	0.08	0.0001	0.08	0.0001
OA Preg	0.03	0.001	0.032	0.002
Senesc - Preg	0.01	0.0042	0.01	0.0001

Notes: Elasticity was derived for each random matrix replicate, and then averaged, and represents the deterministic mean expectation given the mean vital rates. LSA includes process variance in vital rates and as such is a measure of expectation given observed process variance in vital rates.

Table 6-9. Comparison of estimates of population growth rate from deterministic and stochastic (LSA) matrix population models.

	Matrix	LSA
Migrant - λ	0.878	0.866
SD	0.028	0.001
Resident - λ	0.901	0.902
SD	0.027	0.001
$\lambda_M : \lambda_R$	0.976	0.960

Fig. 6-1. 'Mark-resighting' design used for known-fate calf survival estimation. Assuming intrauterine survival = 1.0, the $\phi_{1(neonatal)}$ interval is an average of 45 days, and $\phi_{2(summer-winter)}$ is an average of 250 days. See text for details.

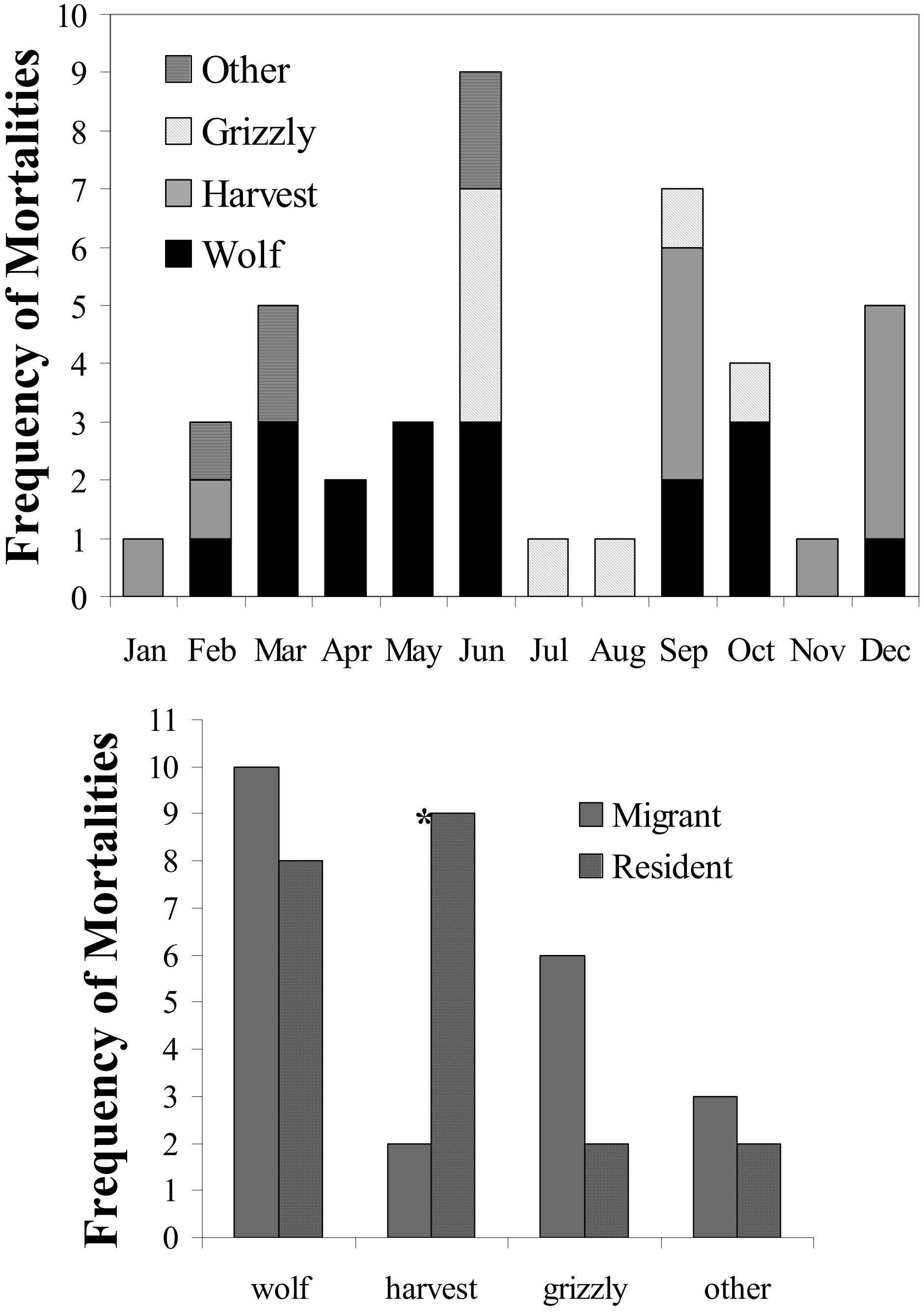


Fig. 6-2. Frequency of adult female elk mortalities by a) mortality cause and b) migratory strategy in the Ya Ha Tinda elk population, Feb 2002 to Nov 2004. Significant differences between mortality causes for migratory strategy are marked with an * (see text for details).

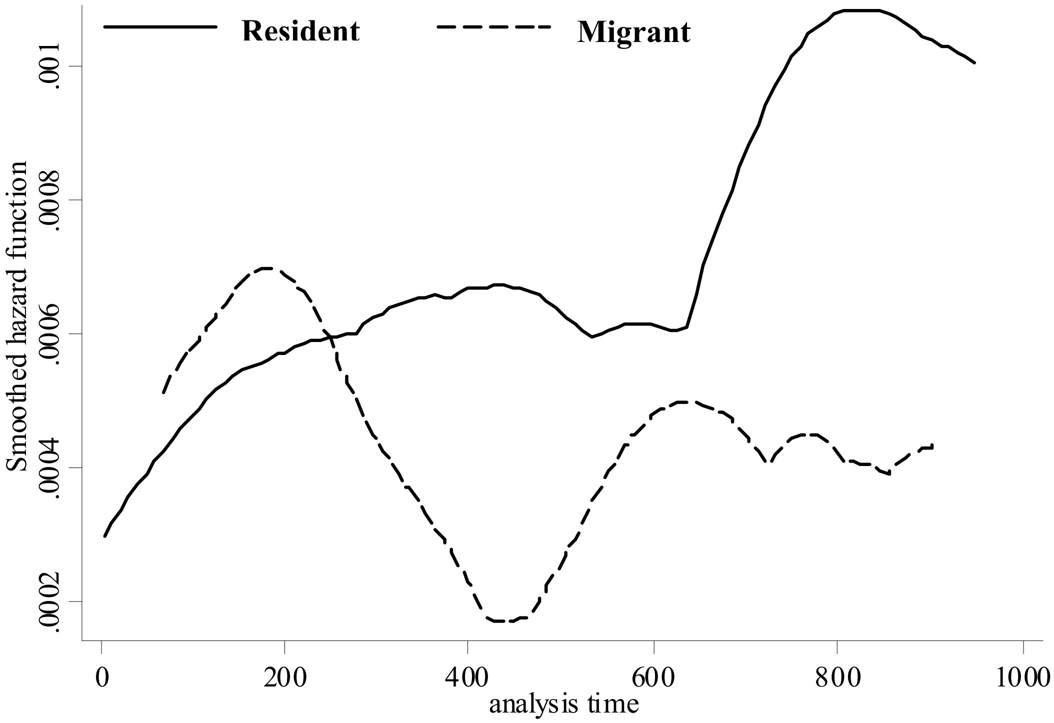


Fig. 6-3. Smoothed interval mortality hazard ($h_{(t)}$) estimates for resident and migrant elk in the eastern slopes of Alberta, Canada, from Feb 2002 (analysis time=0 days since capture) to Nov 2004. Note analysis time indexes survival from capture, which in this graph is dominated by elk entering during Feb/Mar 2002 (analysis time 0), so that time 400 is summer 2003, and time 800 is equivalent to summer 2004.

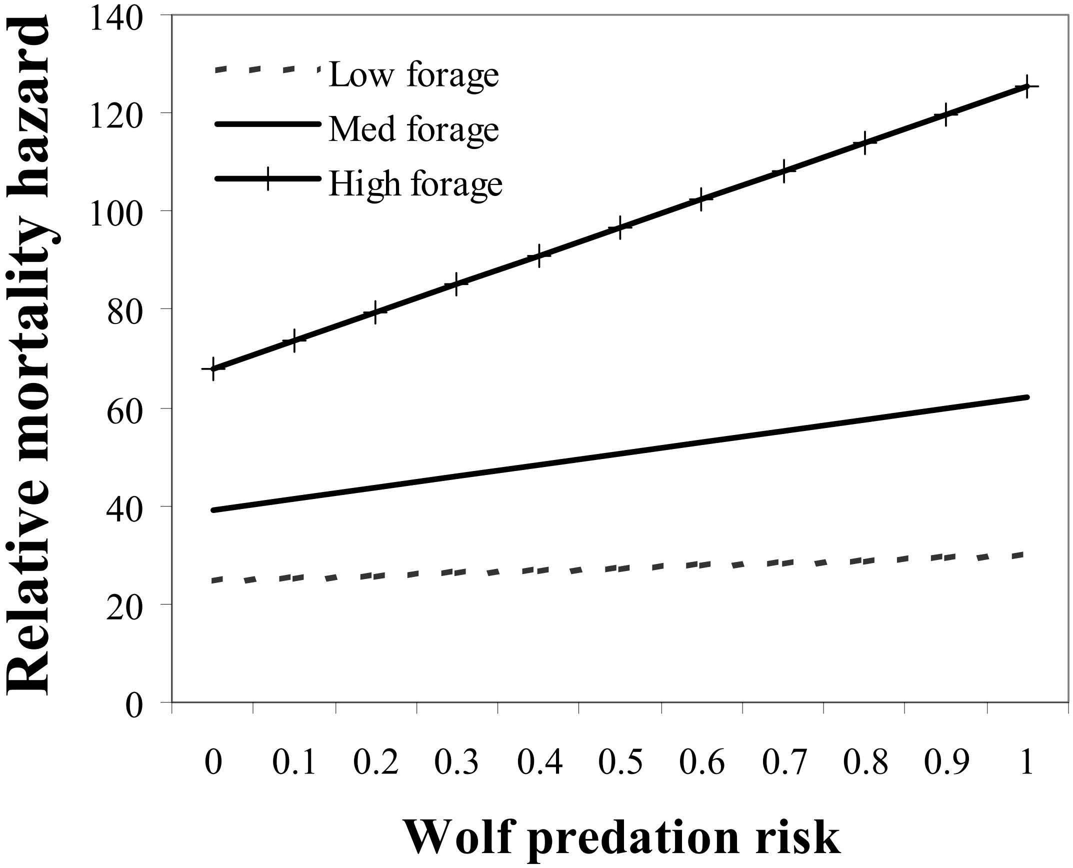


Fig. 6-4. Relative mortality hazard from the top Cox-proportional hazards regression model for migrant and resident adult female elk on the eastern slopes of BNP, Alberta, Canada, 2002-2004. Relative mortality hazard is estimated from $h(t|x_j)= h_0(t)\exp^{(\beta X)}$ at average annual exposure to 5, 25, and 50 g/m^2 of herbaceous forage biomass across relative wolf predation risk.

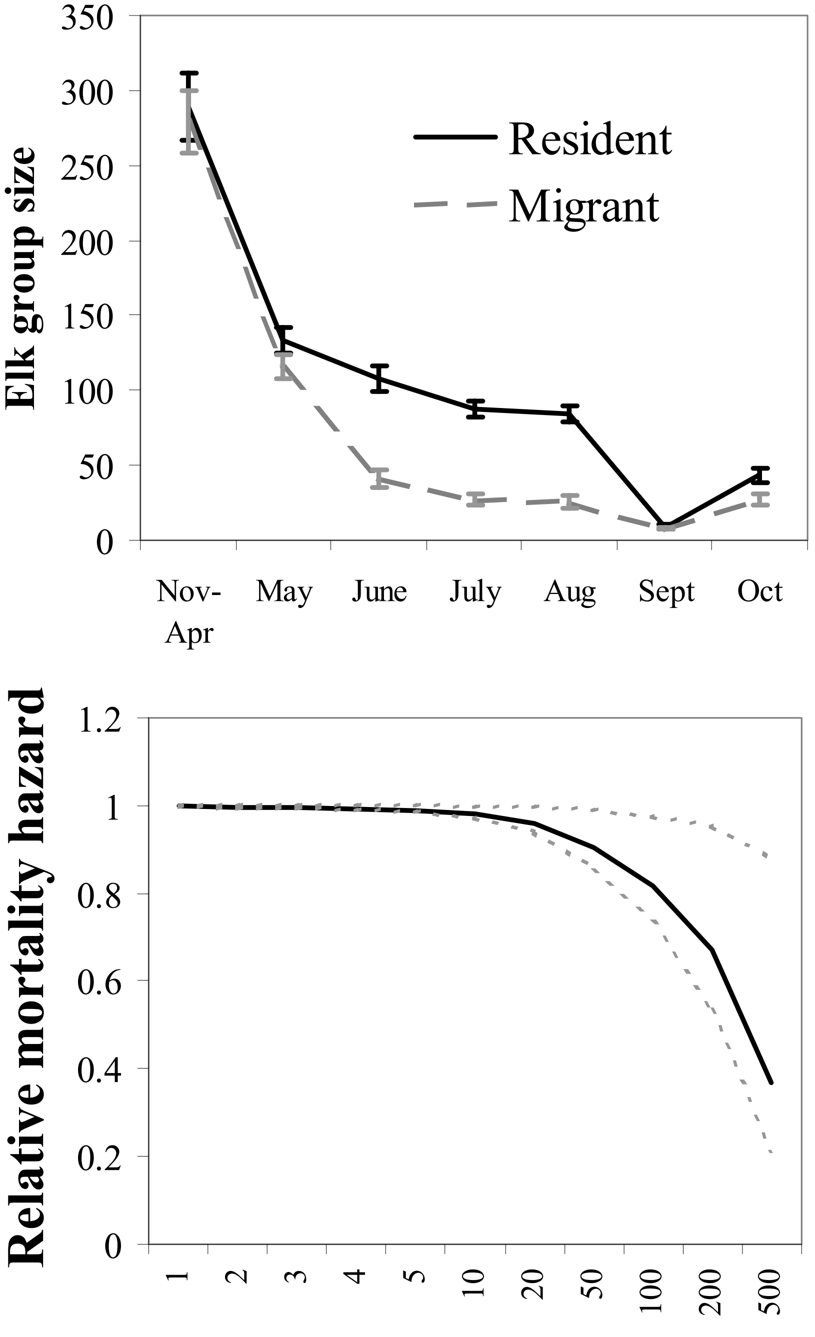


Fig. 6-5. Adult female migrant and resident elk a) seasonal group size relationships (+95% CI) and b) relative mortality hazard (+95%CI) from the top Cox-proportional hazards survival models, eastern slopes of BNP, Alberta, 2002-2004.

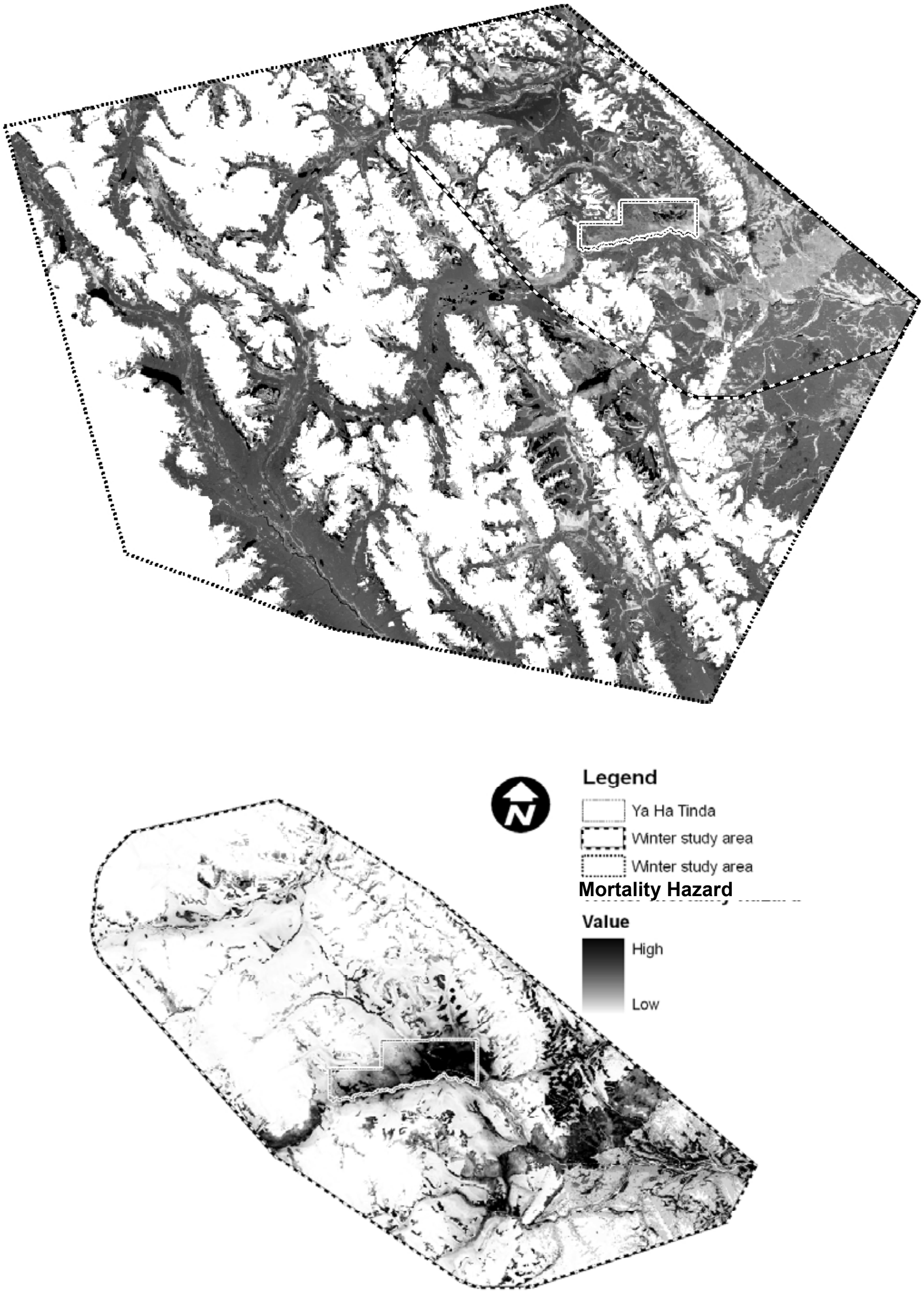


Fig. 6-6. Spatial predictions of relative mortality hazard rate from the top Cox-proportional hazard model ($h(t|x_j)= h_0(t)\exp^{(\beta X)}$) for adult female migratory and resident elk in the eastern slopes of BNP during a) summer and b) winter, 2002-2004.

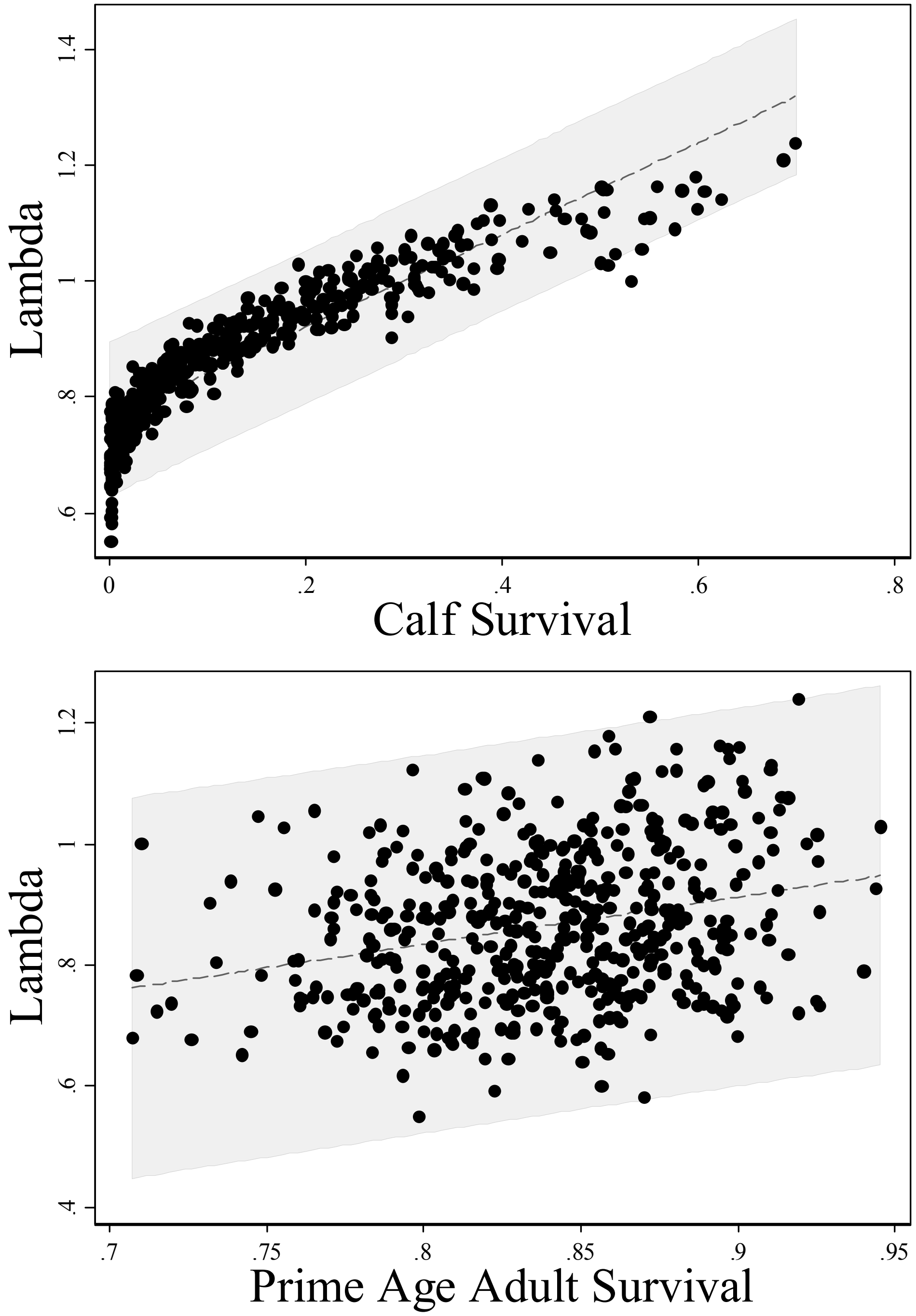


Fig. 6-7. Population growth rate (finite, lambda λ) of migrant elk as a function of the two most important vital rates, a) calf survival and b) prime-aged adult female survival, for explaining variance in elk population growth from 500 simulated matrix models from life-stage sensitivity analysis based on within-study process variance in vital rates from (Raithel et al. 2006).

LITERATURE CITED

Adriaensen, F. and A.A. Dhondt. 1990. Population-dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. Journal of Animal Ecology **59**:1077-1090.

Albon, S.D. and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos **65**:502-513.

Andersen, P.K. and R.D. Gill. 1982. Cox's regression model for counting processes: a large sample study. The Annals of Statistics **10**:1100-1120.

Andersen, R. 1991. Habitat deterioration and the migratory behaviour of moose (*Alces-alces*) in Norway. Journal of Applied Ecology **28**:102-108.

Baker, R.R. 1978. The evolutionary ecology of animal movement. Hodder and Stoughton, London.

Ball, J.P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose (*Alces alces)* ranges in northern Sweden. Wildlife Biology **7**:39-47.

Barber, S.M., L.D. Mech, and P.J. White. 2005. Yellowstone elk calf mortality following wolf restoration: Bears remain top summer predators. Yellowstone Science **13**:37-44.

Bergerud, A.T., H.E. Butler, and D.R. Miller. 1984. Antipredator tactics of calving caribou - dispersion in mountains. Canadian Journal of Zoology **62**:1566-1575.

Beringer, J., L.P. Hansen, W. Wildling, J. Fischer, and S.L. Sheriff. 1996. Factors affecting capture myopathy in white-tailed deer. Journal of Wildlife Management **60**:373-380.

Berthold, P. 2001. Bird migration: a novel theory for the evolution, the control and the adaptability of bird migration. Journal Fur Ornithologie **142**:148-159.

Bonefant, C., J M. Gaillard, F. Klein, and J L. Hamann. 2005. Can we use the young:female ratio to infer ungulate population dynamics? An empircal test using red deer *(Cervus* *elaphus)* as a model. Journal of Applied Ecology **42**:361-370.

Boyce, M.S. 1991. Migratory behaviour and management of elk (*Cervus elaphus*). Applied Animal Behaviour Science **29**:239-250.

Burcham, M., W.D. Edge, and C.L. Marcum. 1999. Elk use of private land refuges. Wildlife Society Bulletin **27**:883-839.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, Massachusetts.

Chen, Y.H. 2002. Cox regression in cohort studies with validation sampling. Journal of the Royal Statistical Society Series B-Statistical Methodology **64**:51-62.

Cleves, M.A., W.W. Gould, and R.G. Gutierrez. 2002. An introduction to survival analysis using Stata. Stata Press, STATA Corporation, College Station, TX, USA.

Cook, R.C., J.G. Cook, D.L. Murray, P. Zager, B.K. Johnson, and M.W. Gratson. 2001. Nutritional condition models for elk: which are the most sensitive, accurate, and precise? Journal of Wildlife Management **65**:988-997.

Cook, R.G. 2002. Nutition and food. Pages 259-350 *in* D. E. Toweill and J. W. Thomas editors. North American elk: ecology and management. Smithsonian Institution Press, Washington.

Coulson, T., J M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology **74**:789-801.

Cox, D.R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B- Statstical Methodology **34**:187-220.

Craighead, J.J., G. Atwell, and B.W. O'Gara. 1972. Elk migration in and near Yellowstone National Park. Wildlife Monographs **29**:1-52.

Dale, B.W., L.G. Adams, and R.T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology **63**:644-652.

Eberhardt, L.L., R.A. Garrott, D.W. Smith, P.J. White, and R.O. Peterson. 2003. Assessing the impact of wolves on ungulate prey. Ecological Applications **13**:776-783.

Festa-Bianchet, M., P. Blanchard, J.M. Gaillard, and A.J.M. Hewison. 2002. Tooth extraction is not an acceptable technique to age live ungulates. Wildlife Society Bulletin **30**:282-283.

Flook, D.R. 1970. Causes of implications of an observed sex differntial in the survival of wapiti. Canadian Wildlife Service Wildlife Service Report No. 11, Ottawa, ON, Canada.

Forbes, G.J. and Theberge, J.B. 1995. Influences of a migratory deer herd on wolf movements and mortality in and near Algonquin Park, Ontario. Pages 303-313 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute,

Frair, J.L.2005. Survival and movement behaviour of resident and translocated wapiti (*Cervus elaphus*): implications for their management in west-central Alberta, Canada. University of Alberta. Edmonton, Alberta, Canada.

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H. M., Stenhouse, G.B., and Beyer, H.L. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology **41**: 201-212. 2004.

Franklin, S.E., G.B. Stenhouse, M.J. Hansen, C.C. Popplewell, J.A. Dechka, and D.R. Peddle. 2001. An integrated decision tree approach (IDTA) to mapping landcover using sattelite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. Canadian Journal of Remote Sensing **27**:579-592.

Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist **138**:478-498.

Fryxell, J.M., J. Greever, and A.R.E. Sinclair. 1988. Why are migratory ungulates so abundant?

The American Naturalist **131**:781-798.

Gaillard, J M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31**:367-393.

Gaillard, J.M. and N.G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology **84**:3294-3306.

Gates, C.C. and R.J. Hudson. 1981. Weight dynamics of wapiti in the boreal forest. Acta Theriologica **26** :407-418.

Gauthier, D.A. and D.G. Larsen. 1986. Predator identification at moose calf mortality sites, southwest Yukon. Yukon Renewable Resources, Whitehorse, YK.

Geist, V. 1982. Adaptive behavioural strategies. Pages 219-277 *in* J. W. T. D. E. Thomas editor, Elk of North America - ecology and management. Stackpole books, Herrisburg, Penn.

Gibeau, M.L., A.P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the Bow river watershed, Alberta, Canada. Biological Conservation **103**: 227-236.

Haberman, S.J. 1973. The analysis of residuals in cross-classified tables. Biometrics **29**:205-220.

Hamer, D. 1999. Forest fire's influence on yellow hedysarum habitat and its use by grizzly bears in Banff National Park, Alberta. Canadian Journal of Zoology **77:** 1513-1520.

Hamer, D. 1996. Buffaloberry [*Sheperdia canadensis* (L). Nutt.] fruit production in fire-succesional bear feeding sites. Journal of Range Management **49:** 520-529.

Hamilton, W.D. 1971. Geometry for the selfish herd. Journal of Theoretical Ecology **31**:295-311.

Hebblewhite, M. 2005. Predation interacts with the North Pacific Oscillation (NPO) to influence western North American elk population dynamics. Journal of Animal Ecology **74**:226-233.

Hebblewhite, M., P.C. Paquet, D.H. Pletscher, R.B. Lessard, and C.J. Callaghan. 2004. Development and application of a ratio-estimator to estimate wolf killing rates and variance in a multiple prey system. Wildlife Society Bulletin **31**:933-946.

Hebblewhite, M. and D.H. Pletscher. 2002. Effects of elk group size on predation by wolves. Canadian Journal of Zoology **80**:800-809.

Hebblewhite, M., C.A. White, C. Nietvelt, J.M. McKenzie, T.E. Hurd, J.M. Fryxell, S. Bayley, and P.C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology **86**:2135-2144.

Hosmer, D.W. and S. Lemeshow. 1999. Applied survival analysis: regression modeling of time to event data. Wiley, New York, NY, USA.

Houston, A.E., J.M. McNamara, and J.M.C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical transactions of the royal society of London, B. **341**:375-397.

Houston, D.B. 1982. The Northern Yellowstone elk: Ecology and management. Macmillan Publ. Co., New York, NY.

Huete, A., K. Didan, T. Miura, E.P. Rodriguez, X. Gao, and L.G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the Modis vegetation indices. Remote Sensing of Environment **83**:195-213.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park. I. Prey species. Canadian Journal of Zoology **71**:130-139.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American Naturalist **142**:59-81.

Kay, C. E., Patton, B. & White, C. A. 2000. Historical wildlife observations in the Canadian rockies: implications for ecological integrity. Canadian Field-Naturalist, **114:** 561-583.

Lack, D. 1968. Bird migration and natural selection. Oikos **19**:1-9.

Lundberg, P. 1987. Partial bird migration and evolutionarily stable strategies. Journal of Theoretical Biology **125**:351-360.

Lundberg, P. 1988. The evolution of partial migration in birds. Trends in Ecology and Evolution

3:172-175.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Second Edition. Kluwer, Boston, USA.

Mayer, M. S., Fuller, T. K., Deblinger, F. D. & Mcdonald, J. E. 2002. Can low-precision population and survival estimates of deer be accurate? Wildlife Society Bulletin **30:** 440-448.

McGillis, J.R.W. 1977. Range management of the Ya Ha Tinda. CWS File #77-13, Canadian Wildlife Service, Edmonton, Canada.

McInenly, L.E.2003. Seasonal effects of defoliation on montane Rough Fescue (*Festuca campestris* Rydb.). University of Alberta. Edmonton, Alberta.

Messier, F. 1994. Unuglate population models with predation: a case study with the North American Moose. Ecology **75**:478-488.

Morgantini, L.E.1988. Behavioural adaptive strategies of wapiti (*Cervus elaphus*) in the Canadian Rocky Mountains. University of Alberta. Edmonton, Alberta.

Morris, W.F. and D.F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Nelson, L.J. and J.M. Peek. 1982. Effect of survival and fecundity on rate of increase of elk. Journal of Wildlife Management **46**:535-540.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy **78**:483-504.

Nielsen, S.E., M.S. Boyce, G.B. Stenhouse, and R.H.M. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience **10**:1-10.

Nielsen, S.E., S. Herrero, M.S. Boyce, R.D. Mace, B. Benn, M.L. Gibeau, and S. Jevons. 2004. Modelling the spatial distribution of human-caused grizzly bear mortalities in the central rockies ecosystem of Canada. Biological Conservation **120**:101-113.

Perez-Tris, J. and J.L. Telleria. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. Journal of Animal Ecology **71**:211-224.

Pulliam, H.R. 1989. Individual behaviour and the procurement of essential resources. Pages 25-38 *in* J. Roughgarden, R. M. May, and S. A. Levin editors. Perspectives in ecology. Princeton University Press, Princeton, USA.

Raedeke, K.J., Millspaugh, J.J., and Clark, P.E. 2002. Population characteristics. Pages 449-491. *in* D. E. Toweill and J. W. Thomas editors. North American elk: ecology and management. Smithsonian Institution Press, Washington.

Raithel, J.D. 2005. Impact of calf survival on elk population dynamics in west-central Montana. University of Montana. Missoula, Montana, USA.

Raithel, J.D., M.J. Kauffman, and D.H. Pletscher. 2006. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management, In Press.

Riggs, M. and Pollock, K.H. 1992. A risk ratio approach to multivariate analysis of survival in longitudinal studies of wildlife populations. Pages 74-89 *in* D. R. McCullough and R. H. Barrett editors. Wildlife 2000: populations. Elsevier Science, London, UK.

Sachro, L.L., W.L. Strong, and C.C. Gates. 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Environmental Management **77**:183-193.

Sasser, G. 1998. One-sample pregnancy diagnosis in elk using fecal steroid metabolites. Journal of Wildlife Disease **34**:126-131.

Singer, F.J., A. Harting, K.K. Symonds, and M.B. Coughenour. 1997. Density dependence, compensation and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management **61**:12-25.

Skrondal, A. and S. Rabe-Hesketh. 2004. Generalized latent variable modeling: multilevel, longitudinal, and structural equation models. Chapman and Hall, New York, NY, USA.

Smith, B. and S.H. Anderson. 1996. Patterns of Neonatal Mortality of Elk in Northwest Wyoming. Canadian Journal of Zoology **74**:1229-1237.

Swingland, I.R. and P.J. Greenwood. 1983. The ecology of animal movement. Oxford University Press, London.

Swingland, I.R. and C.M. Lessells. 1979. Natural regulation of giant tortoise populations on aldabra atoll - movement polymorphism, reproductive success and mortality. Journal of Animal Ecology **48**:639-654.

Testa, J.W. 2004a. Interaction of top-down and bottom-up life history trade-offs in moose (*Alces alces*) Ecology **85**:1453-1459.

Testa, J.W. 2004b. Population dynamics and life history trade-offs of moose (*Alces alces*) in south-central Alaska. Ecology **85**:1439-1452.

Therneau, T.M. and P.M. Grambsch. 2000. Modeling survival data: extending the Cox-model. Springer-Verlag, New York, NY, USA.

Thompson, M.J. and R.E. Henderson. 1998. Elk habituation as a credibility challenge for wildlife professionals. Wildlife Society Bulletin **26**:477-483.

Van Dyke, F.G., W.C. Klein, and S.T. Stewart. 1998. Long-term range fidelity in rocky mountain elk. Journal of Wildlife Management **62**:1020-1035.

Vucetich, J. A., Smith, D. W. and Stahler, D. R. 2005. Influence of harvest, climate, and wolf predation on Yellowstone elk, 1961-2004. Oikos **111:** 259-270.

White, C. A., Hurd, T. L., Hebblewhite, M. and Pengelly, I. R. 2005. Mitigating fire supression, highway, and habitat fragmentation effects in the bow valley ecosystem: preliminary evaluation of a before-after-control-impact (BACI) design with path analysis. In Innes,J. and Jones, G. Monitoring the effectiveness of biological conservation. 2005. Ministry of Forests, Ministry of Water, Air, Lands, University of British Columbia.

White, C. A., Langemann, E. G., Gates, C. C., Kay, C. E., Shury, T. & Hurd, T. E. 2001. Plains bison restoration in the Canadian Rocky Mountains? Ecological and management considerations. Harmon, D. Crossing boundaries to manage wildlife: Proceedings of the 11th Conference on Research and Resource Management in Parks and on Public Lands. Hancock, Michigan, The George Wright Society.

White, C. A., Olmstred, C. E. & Kay, C. E. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Widlife Society Bulletin **26:** 449-462.

White, C., D. Gilbride, M. Scott-Brown, and C. Stewart. 1995. Atlas of the central rockies ecosystem: towards an ecologically sustainable landscape. Komex International Ltd., Calgary.

White, G.C. 2000. Modeling population dynamics. Pages 84-107 *in* S. Demaris and P. R. Krausman editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle Riber, NJ.

White, G.C. and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Supplement **46**:120-138.

White, G.C. and R.A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York.

Wisdom, M.J., L.S. Mills, and D.F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology **81**:628-641.

Woods, J.G. 1991. Ecology of a partially migratory elk population. University of British Columbia.

CHAPTER SEVEN

IMPLICATIONS FOR TRANSBOUNDARY MANAGEMENT OF THE YA HA TINDA ECOSYSTEM

DISSERTATION SUMMARY

In this dissertation, I describe the ecology of a predator-prey system between wolves and a partially migratory elk herd, and the human activities that influence them, in the eastern slopes of Alberta adjacent to Banff National Park (BNP). My focus on the YHT elk was prompted by the perception that migratory behaviour of elk was being lost in this population, similar to migratory declines in the Bow Valley (BV) of BNP (Woods 1991, McKenzie 2001), and in other migratory ungulate populations worldwide (Burcham et al. 1999, Berger 2004). In Chapter 2, I showed evidence for a decline of the M:R ratio in this elk population marshaled from aerial surveys and by comparison with an earlier study (Morgantini 1988). Migratory behaviour of elk changed since the 1970's in three ways: (1) both the proportion and number of elk migrating into BNP declined; the M:R declined from 13:1 in 1980 to 2.5:1 in 2004, and numbers of migrants declined from 980 in 1984 to 580 in 2004; (2) the spatial distribution of migrants changed the most in the front ranges of BNP, and (3) the duration of migration declined because fall migration occurred almost a month earlier. Of eight broad hypotheses proposed to explain these migratory changes, winter range enhancements, access to hay fed to wintering horses, recolonization by gray wolves, and management relocations of elk were most consistent closely associated with observed elk population dynamics and migratory decline. Importantly, prescribed fires, competition with horses for winter forage, and human harvest were unrelated to M:R changes. Additionally, population modeling suggested the long-term equilibrium of about 1000 elk for the YHT under the land management and predation regime observed from 1977-2005. However, given the declining demographic trends in Chapter 6, it seems likely that predator regulation at even lower elk numbers may be possible.

In the remaining chapters of my thesis I examined the potential reasons for the loss of migratory behaviour. Because exploitation of spatial variation in forage is the primary hypothesis for migratory patterns in ungulates, I quantified landscape scale variation in forage quality across the study area using a combination of plot-based and remote-sensing approaches. I showed that migrant summer ranges initially had delayed forage growth by about 2 weeks. Migrants exploited these phenological gradients by selecting intermediate forage biomass to maximize exposure to high forage quality. This resulted in 5% higher average digestibility of forage for migrants, which translated to higher fecal diet quality indexed by higher fecal nitrogen. The magnitude of differences in digestibility between migrants and residents appeared biologically significant, and would be expected to result in higher adult and calf body weights, pregnancy rates, and calf and adult survival rates based on elk nutritional studies (Cook et al. 2004).

In addition to these foraging advantages to migrant elk, migration is typically expected to decrease wolf predation risk for migratory montane ungulates (Seip 1992, Bergerud et al. 1990). However, the decline in migrants noted above in the long-term comparisons over the 1970-2005 period suggested an alternate hypothesis for the effects of wolf predation on migrants. Recolonization of the Central Rockies Ecosystem by wolves starting in the 1980s (Paquet 1993) appeared to be correlated with the loss of migration in the BV (Woods 1991, McKenzie 2001) and also in this study at the Ya Ha Tinda. Therefore, I quantified wolf predation risk across the study area using an approach that incorporated the effects of wolf avoidance of human activity with the effects of wolf distribution, their resource use, and pack sizes. At the landscape scale, migration reduced risk by 70%, primarily because elk left core wolf use areas surrounding den-sites. However, within elk home ranges, residents successfully reduced fine-scale risk to only 15% higher than migrants because wolves avoided high human activity during daytime. Wolf avoidance of high human activity therefore created fine-scale refugia from predation. While migrant elk avoided risk at the largest scales, residents avoided risk at fine scales. These strategies resulted in contrasting foraging trade-offs. Within their summer ranges, migrant elk were ‘free’ to select for areas of intermediate forage biomass, gaining access to higher forage quality. In contrast, residents switched from selecting intermediate forage biomass to selecting maximum forage biomass under increasing predation hazard, which resulted in reduced forage quality. Associated with this switch were the larger group sizes of residents in summer, which reduced mortality hazard of residents by an additional 20% relative to migrants. The larger herd sizes of residents were possible because of the high forage biomass available on the YHT grasslands, which likely accommodated efficient foraging despite increased conspecific interactions (Fortin et al. 2004), although this remains to be demonstrated.

These contrasting resource selection strategies had important consequences to the population dynamics of migrants and residents. Despite foraging benefits of migrating to summer ranges in BNP, migratory elk populations were declining due to predation by wolves and grizzly bears. Resident elk were also declining during this study mainly because of both regulated legal harvest and unregulated legal harvest by treaty First Nations. Human harvest appeared less important for migrants because, firstly, they returned to the YHT mid-way through the hunting season. A second reason may be differential vulnerability to harvest of residents, perhaps as a result of human habituation. For example, because migrants were less vulnerable to human hunting even in the winter, spatial segregation or differential responses to humans between migrants and residents seems likely to exist. This is an important area for research to examine with GPS data of elk already collected. Regardless, accounting for human harvest of female elk over the last 20-years that was 30-50% lower than during this study, resident population growth rates would be at least stable if not increasing.

Nonetheless, fitness balancing between migratory strategies suggested the proportion of residents in the population was increasing at ~2%/year, which was consistent with both long-term trends in the M:R ratio and population counts. Further, I showed that population growth rate of both migratory strategies was most sensitive to calf survival rates. Using the calf survival and adult mortality inferred from earlier studies (Morgantini 1988) in population modeling confirmed the growth of this population to a peak of ~2200 elk observed in the early 1990's would have been possible only under reduced predator mortality. Under the present conditions of high mortality rates, especially for migrant elk, it is difficult to envision migrant declines reversing. Therefore, both the number of and proportion of migrants in this system will likely continue to decline. These trends paralleled population trends in the nearby BV of BNP (Woods 1991, McKenzie 2001) where the proportion of migrants in the population (as well as the numbers of elk, Hebblewhite 2005) rapidly declined to 0.15 following wolf recolonization.

IMPLICATIONS FOR TRANSBOUNDARY MANAGEMENT OF THE YA HA TINDA ECOSYSTEM

Long-term stable states for elk population dynamics and management

Given the high mortality rates of migrant elk revealed in my demographic analysis, both the population size and proportion of migratory elk in the population will likely continue to decline to some low level where numbers are regulated by predation by wolves and grizzly bears. Though there is little specific work on predator regulation in wolf-bear-elk systems, results from this study and a review of the wolf-bear-moose literature supports the interpretation that predation is regulating migrant elk to a low density equilibrium (Orians et al. 1997, Messier 1994, Hayes et al. 2003, Testa 2004). This suggests a long-term stable state under high predator numbers would be low migrant elk densities in the Central Rockies Ecosystem (CRE). Evidence from alternate methods of scientific inquiry also supports this interpretation of the long-term state for low elk densities. Archaeological studies and historical accounts conclude the long-term range of variation for the CRE was characterized by low elk density (White et al. 1998, Kay et al. 2000). For example, Kay et al.'s (2000) review of historical explorer accounts indicates that elk were observed with one-third the frequency of bison, less than one-fifth the frequency of bighorn sheep, and less than one-half the frequency of moose and mountain goats. These frequencies are roughly reversed compared to current relative abundance of ungulates in the ecosystem (Huggard 1993). Notwithstanding potential biases between species, and assuming the historic behaviour of ungulates is similar to today, these observations illustrate the potential for relatively low-density elk populations.

In contrast to migrant elk, without human hunting and lower predation mortality, resident elk appear to have increased both in number and in their proportion in the population. Growth of the resident population occurred because human activities created refugia for prey that has altered predator-prey dynamics at the YHT, similar to the nearby BV (Hebblewhite et al. 2005). At the same time, increased human hunting arising from the special anterless hunt between 2001-2004 likely reduced resident elk population growth rates. Based on archaeological and historic evidence, high resident elk density at YHT may be outside the long-term range of variation (White et al. 1998, Magne et al. 1999, Kay et al. 2000), although locally abundant elk populations certainly existed historically (Martin and Stutzer 1999). However, low resident elk populations in montane systems seems likely considering the ecological importance of human hunting to resident elk survival revealed in this study. This is because the YHT is one of the richest archaeological sites in the Canadian Rockies, revealing a long-history of what was probably year-round hunting by First Nations (Morgantini 1995, White et al. 2001).

The combination of evidence from my demographic analysis, bear-moose-wolf systems, and declines in M:R ratio's in the BV, indicate the present ~50:50 M:R ratio is not stable. Under current wolf and grizzly predation, continued decline in both the proportion and number of migrants seems certain. I hypothesize that the evolutionary stable state for partially migratory elk populations may be either a high proportion of residents or migrants, but not the present even ratio.

The weight of evidence suggests that from a management perspective, migratory declines will be difficult to reverse without dramatic, and long-term, changes to patterns of differential mortality arising from predation by wolves and grizzly bears. Management of resident elk, however, appears more straightforward and amenable to management. Because resident elk appear especially vulnerable to human hunting mortality, re-initiating a limited female-elk hunt that is earlier than the mean migration date for migrant elk (~3 October) would increase mortality of resident elk, and could be used to reduce the size of the resident elk herd. However, because reducing the resident elk population through hunting may be easier than increasing the migrant elk population through manipulation of either forage or predation, reducing resident elk will lead to continued declines of the overall population size. Thus, an alternative to reducing the resident elk herd rapidly through hunting may be required, such as aversive conditioning of elk (Kloppers et al. 2005). One drawback to aversive conditioning is that it will require long-term commitment, similar to the management of the Banff urban elk population (Hebblewhite et al. 2002). A crucial implication for the success of aversive conditioning is the attraction of elk to hay fed to horses. Indeed, I found increasing residents were at least consistent with access to hay, although more detailed analyses of winter spatial relationships of migrant and resident elk is warranted. If aversive conditioning is to be successful, the link between long-term attraction to hay and resident behaviour may be relevant.

EVALUATION OF POTENTIAL MANAGEMENT SCENARIOS

Relative sensitivity to management changes in forage

There was little evidence that the extensive habitat enhancement by prescribed fire in the study area (>200 km^2 of burns) actually translated to increased elk populations or vital rates. This was despite the higher forage biomass in burns (Sachro et al. 2005) and the higher forage quality of migrants in general; migrants still declined due to high wolf and grizzly predation. Furthermore, time-series modeling in Chapter 2 and in White et al. (2005) actually provides limited evidence that burning in areas with high wolf density can actually reduce elk population growth rates. This suggests that the sensitivity of migrant elk to changes in forage via fire will be low. One caveat to this general implication concerns the spatial distribution of fire and predation. In this study, prescribed fires and areas of high predation risk had high overlap, for example in the front ranges of the Cascade, Panther, and Red Deer valleys. This overlap could have countered any benefits from improved resources by increasing mortality of elk. The negative forage-predation interaction I found in both the RSFs and Cox-mortality hazard models supports this interpretation. As a result, a key management hypothesis for improving forage for migrant elk with fire is that prescribed burns should be implemented in areas of low wolf predation risk to maximize benefits to migratory elk. The degree to which this could be successful, however, will depend on the strength with which wolf populations' increase (i.e., the numeric response) following local elk increases (Messier 1994). Burning in low predation risk areas only inhabited seasonally by elk, such as the main ranges of the Rockies or at high elevations, may be the only effective way to decouple local elk and wolf responses following fires.

In contrast, resident elk may be more sensitive to changes in forage biomass for two reasons. First, in Chapter 2, I found broad support for the hypothesis that winter range enhancements increased resident elk. Second, the three-way interaction between larger group sizes decreasing risk in areas of high biomass and high human activity at the YHT also suggests increasing forage biomass near YHT will benefit resident elk. Management implications of the increased sensitivity of residents to forage are clear. Any further enhancements to forage within the ranges of resident elk near the YHT will contribute to the ability of resident elk to make fine-scale trade-offs between risk and forage, *especially* if human activity continues to increase in an unmanaged fashion. Thus, given forage enhancements, resident elk will likely increase. Parks Canada (2005) has proposed two such habitat enhancements on resident ranges: (1) a ~200 ha fire break consisting of logging and partial logging that will increase resident elk forage biomass (Merrill et al. 2004, Munro et al. 2006), and (2) a prescribed fire on the slopes of Hat mountain north of the Ya Ha Tinda, an area used by resident elk in summer. Parks Canada (2005) has recognized the potential for these actions to enhance resident elk, and have proposed aversive conditioning to keep elk groups off-the main grasslands of the YHT. It remains a possible outcome that providing adjacent habitat for resident elk will allow reduced use of the fescue grasslands while maintaining relatively high resident elk numbers. However, there are trade-offs between increasing either resident or migrant elk that may influence the decisions of managers. Increasing resident elk through fires or habitat enhancement near the YHT may be the only way to increase the overall elk population size in the system given constraints on burning imposed by caribou conservation (e.g., not burning in caribou habitat, see below), and constraints on predator management to bolster migrant elk within the National Park. However, increasing resident elk populations may increase wolf densities regionally through the numeric response of wolves to increasing elk density (Messier 1994), which has implications for caribou conservation (see below).

Relative sensitivity of and management constraints to changing wolf predation

The typical conclusion of previous studies of wolf-prey dynamics where wolves regulated or limited prey densities to low numbers was to recommend reduction of predation via large-scale wolf control (Hayes et al. 2003). While there is some controversy over the success of wolf controls (Orians et al. 1997), there is growing experimental evidence that wolf control, when applied consistently to reduce wolf populations by >50% over large areas (>5,000km^2) and time-scales (5-years), can be successful at enhancing ungulate populations (Boertje et al. 1996, Bergerud and Elliot 1998, Hayes et al. 2003, Valkenburg et al. 2004). However, the spatial structure of land management in the study area makes these large-scale and sustained wolf control measures very unlikely (see Fig. 2-1). For example, migrant elk, which suffer the highest mortality from wolves and grizzly bears, migrate into BNP, where wolves, bears and elk are all strictly protected from human caused mortality. There is no precedent within the Canadian National Parks act to allow wolf control within Park boundaries. Moreover, in the successful Yukon wolf controls cited above (Hayes et al. 2003), Parks Canada and the Yukon Territorial Government came to an agreement to not kill any wolves within a set buffer of Kluane National Park (Parks Canada 1995). Given that the viability of both wolves and grizzly bear populations has become a regional concern (Herrero et al. 2000, Callaghan 2002) in the CRE, it seems very unlikely that large-scale wolf controls in or even adjacent to YHT would be implemented.

A second option of reducing wolves only in the area surrounding the YHT may only exacerbate the problem of increasing resident elk population growth rate because: (1) mortality of both migrants and residents was lowest during winter when migrant elk would benefit from any provincial wolf reductions, thus benefits of provincial wolf control would accrue more to residents, and (2) resident elk already have slightly lower wolf mortality than migrants which contributed to their increase. Therefore, despite the potential for elk populations to change in response to changes in wolf predation, the jurisdictional structure of the study area makes it unlikely that wolf populations could be reduced to benefit migrant elk.

A final further question regarding wolf management has to do with the sensitivity of elk to increased predation caused by management restrictions in human activity (see below). If management actions successfully reduced human activity at the YHT, it remains to be tested how effective this would be at increasing wolf predation on elk via the functional components of risk. If the refugium was successfully eliminated through management, increased wolf predation would be expected to decrease resident elk, and both wolf and elk densities would be regulated at low densities. Alternatively, active management to reduce resident elk numbers, through hunting or aversive conditioning (if this increased resident mortality), may achieve the same low-density elk-wolf equilibrium. Research in other systems is starting to suggest the numeric response may drive wolf-prey dynamics more than the functional response (Lessard 2005). Future research should decompose the predation risk models developed in this dissertation to test the sensitivity of predation risk for elk to changes in human use management vs. changes in wolf density itself.

Caribou-wolf-elk dynamics

Patterns of mortality for migrant elk are likely exchangeable with migrant caribou during summer because of the high habitat overlap between the few surviving caribou in BNP and migrant elk. For example, elk#25 was frequently observed within 1 km of the GPS collared caribou#1 during this study, and their summer ranges are virtually identical on the west slopes of the Pipestone River valley. Wolf predation risk during summer (primarily from the Red deer wolf pack) shifted west into the Pipestone River, especially during fall. BNP caribou range is also a regional centre for grizzly bear populations (Herrero et al. 2000). Therefore, the high mortality observed for migrant elk by wolves and grizzly bears is likely the proximate cause of caribou population declines both in BNP and Jasper National Park. This does not bode well for caribou, given that provincial recommendations and recent research all points towards the need to control wolf populations to enhance caribou in areas where forestry (or fire as in BNP) have increased alternate prey populations (moose in AB, elk in BNP)(e.g., Alberta woodland caribou recovery team 2005, Lessard 2005, Lessard et al. 2005, Weclaw and Hudson 2004, Wittmer et al. 2005), and this seems unlikely as discussed above in the National Park context. Caribou's only hope in the National Parks may be reduced elk densities that trigger reduced wolf and grizzly bear densities. Thus, caribou existence may depend on the hypothesized long-term ecosystem state of low elk-predator densities. Whether reduced elk densities, especially of resident elk in 'refugia' populations such as the Banff and Jasper townsites, and indeed at YHT itself are enough to ‘float’ high enough regional wolf densities remains an unknown, but highly relevant, research question.

The role of climatic variability and change

My research suggests several mechanisms by which climatic variability and global climate change may influence migrant and resident elk dynamics. First, climatic variability is likely a long-term factor maintaining partial migration in this population via climatically induced variation in vital rates that differs in effect between strategies. I found climatic signatures in pregnancy rates, calf survival, and potentially, adult survival. Pregnancy rates increased with increasing summer precipitation, and balanced pregnancy rates of strategies. Calf survival was slightly higher in 2004 during a high forage biomass summer, and likewise, adult survival also improved in 2004, but wolf predation risk also was the lowest in 2004. I speculate that because benefits of high forage biomass accrue more to residents and because of resident avoidance of wolves at the YHT that residents may experience greater stochasticity induced by climatic variability.

However, my research also suggested that climate change could disproportionately impact migrants, mainly through differential climatic downscaling between migrant and resident ranges influencing the start of the growing season. Higher precipitation in summer spring may result in higher summer snowfalls during calving for migrants, but not residents, through differential effects on higher elevation migrant ranges (sensu Pettorelli et al. 2005), which would influence calf survival (Coulson et al. 1997). Phenological variation induced by climate change in montane systems may also similarly influence migrants because their calf survival may be more closely tied to plant phenology. However, long-term studies are required to really investigate the suggestions presented by this research about how climate change may influence elk.

Implications for human-use management

One of the largest, but most difficult to quantify, long-term changes in the system has been the steady increase in human recreational activity at the YHT since the early 1970's. Human activity at the YHT has changed from a regional backwater in the 1970's with human activity focused in hunting season to the YHT being touted as one of Alberta's premier horse-back recreation destinations with two campgrounds with hundreds of camping sites between them. As an example, between 1 May and 30 September of 2002 there was an average of 116 and 85 people and horses, respectively, using the Bighorn campground each night, for a total of 13,619 and 9,789 person and horse nights of use (Parks Canada, unpubl. data). Moreover, there are very few guidelines for human activity both on the YHT ranch itself and surrounding Forest Land Use Zones (FLUZ) in terms of random camping, trail restrictions, etc. Finally, there is growing regional preassure to provide increased Off-Road-Vehicle (ORV) recreational opportunities even in the FLUZ's, for example, snowmobiling access into upper Scalp Creek.

While the YHT falls within the Bighorn Access Management Plan, which guides *patterns* of human activity of the areas surrounding the YHT, there were very few guidelines regarding the *amount* of human activity permitted. My research indicates that the amount of human activity in the YHT area presently surpasses ecological thresholds under modern human use patterns. Active management to maintain human activity may be required, for example, through managing human use similar to similar successful efforts in the BV (Duke et al. 2001). It is clear that managers must (1) acknowledge that the unfettered growth of human activity at the YHT will continue to increase in the future amplifying the negative ecological impacts detailed in this study, and (2) take active steps to reduce and/or manage human activity in the YHT area. Failing to do so may result in the region being ‘loved to death’. While Parks Canada has jurisdiction to manage human activity on the ranch, clearly Alberta has control over regional human activity, and the coordinated approach of human activity in this region should be a first priority of both management agencies.

FUTURE MANAGEMENT OF THE YA HA TINDA RANCH

In discussing the long-standing controversy over the jurisdictional complexity of the Ya Ha Tinda, I draw on my review of decades of Parks Canada files at the Calgary regional office regarding management of the Ya Ha Tinda. First, I think it is crucial to acknowledge that in terms of ecosystem management track record, Parks Canada clearly has a winning record in the province of Alberta. It is simply the primary focus of Parks Canada to manage for ecological integrity, whereas it is the province of Alberta’s focus to manage for both ecological and economic factors. For example, during my brief tenure at the YHT, Parks Canada turned down at least two applications to allow snowmobiling/ORV use on the YHT that may have been difficult for provincial agencies to refuse alone. Second, on a longer and larger scale, the YHT is one of the last and best-preserved montane rough fescue grasslands precisely because it has been retained by Parks Canada since the 1930’s. Given the rapacious appetite for resource extraction along Alberta’s east slopes (Timoney and Lee 2001), there is little reason to believe that had the

YHT reverted to provincial ownership in the 1930's the YHT would be as well preserved as it is today.

However, in my view, the real debate is not whether Parks Canada or AB-SRD, or alternately, some third party such as Rocky Mountain Elk Foundation or the Nature Conservancy should manage the YHT. The real problem with and failing of previous management of the YHT is the lack of *certainty* with which Parks Canada has managed the YHT (sensu Clark 1999). Every five-years or so starting in the 1970's when the Department of Defense made an inquiry into purchasing the YHT, Parks Canada has gone through some internal machinations to define what the YHT is both ecologically and operationally, with various decisions to keep, sell, or ignore the YHT being made over the ensuing years. Following each particular controversy surrounding management of the YHT, I detected the following recurring theme; (1) managers would get agitated about some issue at the YHT, (2) study the problem (as I have done in this Dissertation), then (3) make recommendations to improve management, many of which echo precisely the recommendations made in this dissertation. At this crucial juncture following the delivery of management recommendations, I noted that time and time again in the Parks Canada files, the uncertainty over the status of the YHT, and the 'fear' of attracting undue bureaucratic attention to this dust-covered jewel of the Canadian Rockies National Parks impeded implementation of many of the needed management recommendations. I therefore conclude that it is not really a question of who should manage the YHT, but *how*. I believe that if the YHT had a more certain and recognized status as more than just some private ranchlands owned by Parks Canada, this would provide the firm foundation from which to generate a new management plan and direction for the YHT, the ecological heart of BNP. Lack of management certainty, both in terms of defining management objectives and intergovernmental relationships, has been recognized as a key impediment to effective interagency management (Clark 1999, Kelson and Lilieholm 1999, Pedynowski 2003). Permanent recognition and status within the National Park system should not mean that it should be protected as a National Park. Indeed, given the pressures facing the YHT from human activity outlined in this dissertation, I believe that National Park designation would only exacerbate any ecological problems. More flexible, yet permanent, status could be achieved through a variety of mechanism under Federal management, such as through the National Historic Sites or National Game Sanctuaries Act used in the Arctic (i.e., Thelon Game Sanctuary). Certainly, the YHT is home to not only valuable ecological, but archaeological, historical, and cultural resources that all require more certainty with management as the eastern slopes of Alberta undergo continued growth and development in the 21st century.

With a firm foundation for the Ya Ha Tinda, Parks Canada and Alberta could focus attention on the real management challenge: How do Park and Provincial managers harmonize management objectives across Park boundaries for this elk population, while accounting for the cumulative effects of human activity and natural processes such as fire? When one agency, Parks Canada, manages for ecological integrity in one part of the ecosystem, long-term declines in elk density may be consistent with their long-term management objectives. However, in the Alberta side of the ecosystem, management objectives include both consumptive and non-consumptive wildlife use. For example, the YHT is identified as one of the province’s key elk hunting areas for both residents and non-resident hunters (Gunson 1997), recognized as a major contributor to local and regional economies. In this context then, low-density population of elk may not meet Provincial management objectives. The difficulty in transboundary systems is in defining common management goals and targets despite different management 'paradigms' (Clark 1999, Pedynowski 2003). The statistical models developed in this dissertation provide exactly the spatially-explicit framework required to direct transboundary management in this complex setting (Johnson et al. 2005) *once* management goals and objectives have been agreed upon between management agencies. I believe this jointly defining management objectives for the YHT elk population would be a beneficial step to help define a consensus approach to managing the YHT. The lack a common problem definition between management agencies itself may be the biggest obstacle to overcome (Clark 2000, Clark et al. 2001) before useful application of the statistical framework presented in this research. In the similarly complex transboundary Jackson Hole elk population, Clark et al. (2000) concluded exactly that the lack of an effective 'commons' framework for problem definition and management objectives had contributed to management conflicts. Therefore, a management planning process to define management objectives for the YHT across jurisdictions (*sensu* Clark et al. 2000) appears a useful first step before application of the statistical models developed in this dissertation can be applied by both management agencies to manage the Ya Ha Tinda elk population.

LITERATURE CITED

Alberta Woodland Caribou Recovery Team. 2005. Alberta woodland caribou recovery plan, 2004/05 - 2013/14. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, AB, Canada. Alberta species at risk recovery plan number 4.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals.

Conservation Biology **18**:320-331.

Bergerud, A.T. and J.P. Elliot. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. Canadian Journal of Zoology **76**:1551-1569.

Bergerud, A.T., R. Ferguson, and H.E. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behaviour **39**:360-368.

Boertje, R.D., P. Valkenburg, and M.E. McNay. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management **60**:474-489.

Burcham, M., W.D. Edge, and C.L. Marcum. 1999. Elk use of private land refuges. Wildlife Society Bulletin **27**:883-839.

Callaghan, C.2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival, and persistence in the Central Rocky Mountains, Canada. Department of Zoology, University of Guelph. Guelph, ON.

Clark, T.W. 1999. Interdisciplinary problem-solving: next steps in the Greater Yellowstone Ecosystem. Policy Sciences **32**:393-414.

Clark, T.W. 2001. Wildlife resources: the elk of Jackson Hole, Wyoming. Pages 91-108 *in* J. Burger, E. Ostrom, R. B. Norgaard, G. Policansky, and B. D. Goldstein editors. Protecting the commons: a framework for resource management in the Americas. Island Press, New York, New York, USA.

Clark, T. W., Casey, D., and Halverson, A. 2000. Developing sustainable management policy for the National Elk Refuge, Wyoming. 2000. New Haven, Conneticut, Yale University. Bulletin Series, Yale School of Forestry and Environmental Studies.

Cook, J.G., B.K. Johnson, R.C. Cook, R.A. Riggs, T. Delcurto, L.D. Bryant, and L.L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs **155**: 1-61.

Coulson, T., S. Albon, F. Guiness, J. Pemberton, and T. Clutton-Brock. 1997. Population substructure, local density, and calf winter survival. Ecology **78**:852-863.

Duke, D.L., Hebblewhite, M., Paquet, P.C., Callaghan, C., and Percy, M. 2001. Restoration of a large carnivore corridor in Banff National Park. Pages 261-275 *in* D. S. Maehr, R. F. Noss, and J. L. Larkin editors. Large mammal restoration: ecological and sociological challenges in the 21st century. Island Press, Washington.

Fortin, D., M.S. Boyce, and E.H. Merrill. 2004. Multitasking by mammalian herbivores: overlapping processes during foraging. Ecology **85**:2312-2322.

Gunson, J.R. 1997. Elk management plan for Alberta. Wildlife Management Division, Alberta Environmental Protection, Natural Resource Service, Edmonton.

Hayes, R.D., R. Farnell, R.M.P. Ward, J. Carey, M. Dehn, G.W. Kuzyk, A.M. Baer, C.L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the yukon: ungulate responses and management implications. Wildlife Monographs 152: 1-35.

Hebblewhite, M., D.H. Pletscher, and P.C. Paquet . 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology **80**:789-799.

Hebblewhite, M., C.A. White, C. Nietvelt, J.M. McKenzie, T.E. Hurd, J.M. Fryxell, S. Bayley, and P.C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology **86**:2135-2144.

Herrero, S., P.S. Miller, and U.S. Seal. 2000. Population and habitat viability assessment for the grizzly bear of the Central Rockies Ecosystem (*Ursus arctos*). Eastern Slopes Grizzly Bear Project and Conservation Breeding Specialist Group, IUCN/SSC, Apple valley, Minnesota, USA.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Park. I. Prey species. Canadian Journal of Zoology **71**:130-139.

Johnson, C.J., M.S. Boyce, R.L. Case, D.H. Cluff, R.J. Gau, A. Gunn, and R. Mulders. 2005.

Cumulative effects of human developments on arctic wildlife. Wildlife Monographs **160**:1-36.

Kay, C.E., B. Patton, and C.A. White. 2000. Historical Wildlife Observations in the Canadian Rockies: Implications for Ecological Integrity. Canadian Field-Naturalist **114**:561-583.

Kelson, A.R. and R.J. Lilieholm. 1999. Transboundary Issues in Wilderness Management. Environmental Management **23**:297-305.

Lessard, R.B. 2005. Conservation of woodland caribou (*Rangifer tarandus caribou*) in west-central Alberta: a simulation analysis of multi-species predator-prey systems. University of Alberta. Edmonton, Alberta, Canada.

Lessard, R.B., S.J.D. Martell, C.J. Walters, T.E. Essington, and J.F. Kitchell. 2005. Should ecosystem management involve active control of species abundances? Ecology and Society **10**:1-21. [URL] http://www.ecologyandsociety.org/vol10/iss2/art1/

Magne, M. 1999. Archaeology and Rocky Mountain ecosystem management: theory and practice. The George Wright Forum **16,** 66-76.

Martin, P.S. and C.R. Stutzer. 1999. War zones and game sinks in Lewis and Clarks ' west. Conservation Biology **13**:36-45.

McKenzie, J.A. 2001. The selective advantage of urban habitat use by elk in Banff National Park. University of Guelph. Guelph, Ontario.

Merrill, E.H., D. Visscher, H. Beyer, J. Frair, D. Fortin, M.S. Boyce, and J.R. Allen. 2004. Vegetation map and dynamics of elk forage for the central east slopes elk and wolf study (CESEWS). University of Alberta, Edmonton, Alberta.

Messier, F. 1994. Unuglate population models with predation: a case study with the North American Moose. Ecology **75**:478-488.

Morgantini, L.E.1988. Behavioural adaptive strategies of wapiti (*Cervus elaphus*) in the Canadian Rocky Mountains. University of Alberta. Edmonton, Alberta.

Munro, R., M. Hebblewhite, and E.H. Merrill. 2006. Effects of post-fire logging on elk habitat during the first 3-years post burn. Forest Ecology and Management, In prep.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat Selection and Survival of Mule Deer: Tradeoffs Associated With Migration. Journal of Mammalogy **78**:483-504.

Orians, G., P.A. Cochran, J.W. Duffield, T.K. Fuller, R.J. Gutierrez, W.M. Henemann, F.C. James, P. Kereiva, S.R. Kellert, D. Klein, B.N. McLellan, P.D. Olson, and G. Yaska. 1997. Wolves, bears, and their prey in alaska. National Academy Press, Washington.

Paquet, P.C. 1993. Summary reference document - ecological studies of recolonizing wolves in the central Canadian Rocky Mountains. Prepared by John/Paul & Associates for Parks Canada, Banff National Park Warden Service, Banff, Alberta, 215pp,

Parks Canada. 1995. Memorandum of agreement between the Yukon territorial government and Kluane National Park regarding wolf control options to enhance the Champagne-Aishik caribou population. Parks Canada, Haines Junction.

Parks Canada. 2005. Ya Ha Tinda Ranch fuel break, prescribed fire, elk conditioning, elk proof fencing: Environmental Assesment. Banff Warden Service, Parks Canada, Banff, Alberta, Canada.

Pedynowski, D. 2003. Prospects for ecosystem management in the crown of the continent ecosystem, Canada - United States: survey and recommendations. Conservation Biology **17**:1261-1269.

Pettorelli, N., A. Mysterud, N.G. Yoccoz, R. Langvatn, and N C. Stenseth. 2005. Importance of climatological downscaling and plant phenology for red deer in heterogenous environments. Proceedings of the Royal Society B **272**:2357-2364.

Sachro, L.L., W.L. Strong, and C.C. Gates. 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Environmental Management **77**:183-193.

Seip, D.R. 1992. Factors limiting woodland caribou populations and their relationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology **70**:1494-1503.

Testa, J.W. 2004. Population dynamics and life history trade-offs of moose (A*lces alces*) in south-central Alaska. Ecology **85**:1439-1452.

Timoney, K. and P. Lee. 2001. Environmental management in resource-rich Alberta, Canada: first world jurisdiction, third world analogue? Journal of Environmental Management **3**:387-405.

Turner, M.G., G.J. Arthaud, R.T. Engstrom, S.J. Hejl, J.G. Liu, S. Loeb, and K. Mckelvey. 1995. Usefulness of spatially explicit population-models in land management. Ecological Applications **5**:12-16.

Turner, M.G., Y. Wu, L.L. Wallace, W.H. Romme, and A. Brenkert. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. Ecological Applications **4**:472-496.

Valkenburg, P., M.E. Mcnay, and B.W. Dale. 2004. Calf mortality and population growth in the delta caribou herd after wolf control. Wildlife Society Bulletin **32**:746-756.

Weclaw, P. and R.J. Hudson. 2004. Simulation of conservation and management of woodland caribou. Ecological Modelling **177**:75-94.

White, C.A., T.L. Hurd, M. Hebblewhite, and I.R. Pengelly. 2005. Mitigating fire supression, highway, and habitat fragmentation effects in the bow valley ecosystem: preliminary evaluation of a before-after-control-impact (BACI) design with path analysis. I*n* Innes, J. and Jones, G., editors. Monitoring the effectiveness of biological conservation. Ministry of Forests, Ministry of Water, Air, Lands, University of British Columbia,

White, C.A., E.G. Langemann, C.C. Gates, C.E. Kay, T. Shury, and T.E. Hurd. 2001. Plains bison restoration in the Canadian Rocky Mountains? Ecological and management considerations. *In* Harmon, D., editor. Crossing boundaries to manage wildlife: Proceedings of the 11th Conference on Research and Resource Management in Parks and on Public Lands. The George Wright Society, Hancock, Michigan.

White, C.A., C.E. Olmsted, and C.E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Widlife Society Bulletin **26**:449-462.

Wittmer, H.U., A.R.E. Sinclair, and B.N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia **144**:257-267.

Woods, J.G.1991. Ecology of a partially migratory elk population. University of British Columbia, Vancouver, BC.