

University of Alberta

Woodland caribou conservation in the Little Smoky:
wolf management and the role of bears

by

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DEDICATION

This work is dedicated to my grandparents, George and Lorraine Benoit, who instilled in me an appreciation for nature and the outdoors. I will always cherish memories of time spent together hiking through the woods, picking wild berries, and fishing in the brook.

ABSTRACT

Woodland caribou population declines in west-central Alberta precipitated a wolf-control program. This program to protect caribou could be compromised if (1) there are strong public pressures against helicopter gunning and strychnine poisoning of wolves and/or (2) other predators compensate to kill caribou. Because bears can be important ungulate predators, I used stable isotope techniques to reconstruct black and grizzly bear diets including contributions of caribou, caribou calves, ants, ungulates (moose, deer and elk), and 3 plant groups. Bears assimilated 2-58% terrestrial protein indicating large variation among individuals. As an alternative to current wolf-control practices, I reviewed spatial and temporal patterns of harvests (1985-2006) on registered traplines. Wolf trapping has increased during the past 2 decades, but on average trappers harvested only 10% of the provincial wolf population, well below culls required to control the population. Under the registered trapline system it is unlikely that trapping could control wolf abundance.

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CHAPTER 1: GENERAL INTRODUCTION

BACKGROUND

Boreal woodland caribou (*Rangifer tarandus caribou*) are listed as threatened in Canada according to the Committee on the Status of Endangered Wildlife in Canada (Thomas and Gray 2002). The boreal population is made up of herds located across the northern boreal forest of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Newfoundland-Labrador, and the Northwest Territories (Figure 1–1). Reasons for the formal listing include: population declines throughout the range, habitat loss, and increased predation believed to be linked to human activity (Vors and Boyce in press). Declines in North American caribou populations occurred in the late 1800s and early 1900s following human settlement (Bergerud 1974); however, early scientific reports documenting declines in Canada were only published in the 1950's (e.g., de Vos and Peterson 1951, Edwards 1954, and see Bergerud 1974). Declines were documented in Alberta in the mid to late 1980s (Edmonds and Bloomfield 1984, Edmonds 1988).

The designation of caribou as ‘threatened’ has resulted in recovery planning in nine different jurisdictions. Alberta, Manitoba, and Labrador have published recovery plans, draft recovery plans have been prepared for Canada (Environment Canada 2008), British Columbia, Saskatchewan, Ontario, and Quebec, while the Northwest Territories have put in place a recovery team. Alberta currently has 18 caribou herds, 14 of which are boreal ecotype (Figure

1–2). The Alberta woodland caribou recovery plan lists three herds that are at immediate risk of extirpation: the North Banff, Slave Lake, and Little Smoky populations (Alberta Woodland Caribou Recovery Team 2005). The Little Smoky is the herd of interest for this thesis due to current conservation efforts aimed at rescuing the endangered population.

Two ecotypes are found in Alberta, boreal and mountain, that differ in their habitat use (Dzus 2001). Mountain caribou migrate to high-elevation alpine habitats in the spring and return to foothill forests in the fall. Boreal caribou do not show this migratory behaviour, rather they inhabit boreal forest where they make extensive movements throughout the year (Stuart-Smith et al. 1997).

Woodland caribou feed primarily on lichen, although they consume various vascular plants in spring and summer (Edmonds and Bloomfield 1984, Thomas and Gray 2002). Because lichen cover is directly correlated with forest stand age (Dunford et al. 2006), caribou largely depend on continuous tracts of mature to old growth forests to meet their foraging requirements. In Alberta, boreal ecotype caribou are often found in peatland (muskeg) complexes dominated by black spruce (*Picea mariana*) and larch (*Larix laricina*; Fuller and Keith 1981, Bradshaw et al. 1995, Anderson 1999). Caribou movement generally is restricted the boundaries of peatland complexes (Stuart-Smith et al. 1997) and treed bogs are selected even when peatlands are interspersed within an upland habitat mosaic (Anderson 1999). By exploiting a nutrient-poor niche caribou might be avoiding competition with other ungulates unable to use these habitats (Thomas and Gray 2002). Caribou habitat selection and use is thought to be

closely linked to their anti-predator tactic through the spatial separation hypothesis (James et al. 2004), which predicts that there is little overlap between preferred habitats of predators and their prey. Caribou may avoid predators, notably wolves (*Canis lupus*), by occurring in low densities (individually or in small groups) and by seeking refuge in contiguous forest seldom used by other ungulates (Bergerud 1974, Bergerud and Elliot 1986, Bergerud and Page 1987, Seip 1992). James et al. (2004) found support for the spatial separation hypothesis observing that caribou selected fen/bog complexes while wolves and moose (*Alces alces*) selected well-drained habitats. This difference in habitat selection resulted in spatial separation and in turn reduced wolf predation pressure on caribou. Further, Stuart-Smith et al. (1997) showed that calf survival was lower in landscapes with smaller patches of fen and a higher proportion of upland habitat.

Breeding of woodland caribou occurs in late-September and October and most adult females (older than one year) produce a calf in May or early June (Thomas and Gray 2002). Boreal caribou, unlike barren-ground caribou, do not have easily identifiable calving sites (Dzus 2001). Pregnant cows in west-central Alberta disperse on the landscape and calve in diverse habitats including alpine, subalpine forest, treed and open muskeg (Edmonds and Smith 1991). Females generally calve individually to reduce the risk of predation (Bergerud et al. 1984). Calf mortality in the first months of life is particularly high. Fuller and Keith (1981) reported an average mortality of 58% in first 2 months of life in northeastern Alberta, and Bergerud and Elliot (1986) reported an average

mortality of 55% (79-13%) by the end of calving season. Calf recruitment is generally low as 50-80% of calves die within the first year of life (Fuller and Keith 1981, Thomas and Gray 2002). Low calf recruitment has been largely attributed to predation typically from gray wolves (Bergerud and Elliot 1986, Bergerud and Page 1987, Seip 1992, Wittmer 2005), but other predators such as golden eagles (*Aquila chrysaetos*), wolverine (*Gulo gulo*), and bears (*Ursus* spp.) also play a role in calf survival (Gustine et al. 2006). Adult survival is usually much higher, with average survival rates ranging from 79-92% in Alberta, Saskatchewan and British Columbia (Fuller and Keith 1981, Bergerud and Elliot 1986, Stuart-Smith et al. 1997, Rettie and Messier 1998, McLoughlin et al. 2003).

The boreal ecosystem has a natural-fire regime with fires occurring every 29 to 142 years depending on vegetation cover (Larsen 1997). Wildfires can change the landscape quickly by reducing the amount forage available for forest-dwelling animals such as woodland caribou. Dalerum et al. (2007) reported that decreased availability of lichen following a fire did not affect caribou home range size and location, nor did it affect annual mortality or fecundity. This pattern held true even with up to 76% of the home range burned, suggesting that caribou might be resilient to the effects of fire, perhaps because of their large home-range size (Dalerum et al. 2007).

IMPACTS OF INDUSTRIAL ACTIVITY

Woodland caribou are sensitive to human activity and are thought to be negatively impacted by industrial activity (Bradshaw et al. 1997, McLoughlin et al. 2003,

Vistnes and Nellemann 2008). Development associated with the forestry and energy sectors can affect caribou through physical barriers to movement (Klein 1971), vehicle and poaching related mortalities (Johnson 1985), direct habitat loss, functional habitat loss through avoidance of human infrastructure (Vistnes and Nellemann 2008), and habitat alteration and associated apparent competition (Wittmer et al. 2007).

In particular, the oil and gas industry impacts caribou through the creation of roads, seismic lines and infrastructure (e.g., pipelines, wells, compressor stations). Roads affect caribou by acting as barriers to movement (Dyer et al. 2002) and by increasing access for poachers (Johnson 1985). Seismic lines and low-use roads increase travel and hunting efficiency of wolves as they are able to travel three times faster by using these linear corridors (James 1999, James and Stuart-Smith 2000). James and Stuart-Smith (2000) found that locations of caribou mortalities were on average closer to seismic lines than live locations indicating that caribou are exposed to higher mortality risk near linear features. Dyer et al. (2001) found that caribou in northeastern Alberta avoided well sites, seismic lines, and roads and that as a result 22-48% of the landscape had reduced caribou use (i.e., functional habitat loss). Noise associated with oil and gas infrastructure has been linked to increases in caribou energetic costs due to increased movement around human infrastructure (Bradshaw et al. 1998). The most obvious effect of the forestry industry is direct habitat loss due to logging of mature forests. Courtois et al. (2007) associated lower caribou survival probability with increased proportion of early seral forest cover within caribou

home ranges. Smith et al. (2000) reported that caribou were 1.2 km farther from new cut blocks than random points on the landscape indicating some functional habitat loss in addition to the direct removal of habitat.

Cumulative effects of natural and industrial disturbances have been linked to the finite rate of caribou population change (λ). Sorensen et al. (2008) developed a model that predicted 96% of the variability in λ using two variables: percentage of caribou range within 250m of anthropogenic features, and percentage of caribou range burned in the last 50 years. A threshold of 61% of caribou range within 250m of anthropogenic features was identified as the maximum industrial footprint that could ensure sustainable caribou populations (Sorensen et al. 2008).

Although declines in caribou populations have been largely attributed to industrial development, the main limiting factor on populations appears to be increased predation rates by wolves (see Fuller and Keith 1981, Bergerud and Elliot 1986, Wittmer et al. 2005). Increased caribou predation is associated with large-scale changes in habitat structure and changes in species composition. Linear features increase predator efficiency and may also provide greater access by predators to caribou ranges, thereby increasing the predation risk (Stuart-Smith et al. 1997, James 1999, James and Stuart-Smith 2000). The removal of late seral forest cover returns the habitat to an early successional stage, reduces the amount of caribou habitat, and creates greater browse and habitat for species such as moose, elk (*Cervus elaphus*), and deer (*Odocoileus* spp). The abundance of food available in younger stands facilitates increases in these other ungulate

populations (Rempel et al. 1997) which in turn provides abundant prey for predators and allows predators to occur at higher densities (Schwartz and Franzmann 1991, Ballard et al. 2000). The current hypothesis is that caribou population declines are mediated by an indirect interaction between habitat change and caribou through other prey species and their shared predators (Witmer et al. 2007). This direct interaction between prey populations is known as apparent competition (Holt 1977, Holt and Lawton 1994).

LITTLE SMOKY CARIBOU HERD

The Little Smoky (LSM) caribou herd is located in the foothills of west-central Alberta east of Grande Cache and west of Fox Creek between highways 40 and 43 (Figure 1–2). The caribou range covers an approximate area of 3,000 km² and spans mostly over two wildlife management units (WMUs): 352 and 353. Aerial survey data demonstrate a decline of approximately 70% in the number of females between 1990 and 2007 (WCCLPT 2008). Smith (2004) modeled the population trajectory of female caribou over 20 years and forecast a decline of about 77% by 2024. The current population estimate is 80 individuals (WCCLPT 2008).

The LSM range has the highest level of development of any caribou herd in Canada (Environment Canada 2008). There are currently three forest management agreements within the Little Smoky range (Canadian Forest Products Ltd., Alberta Newsprint Co., and West Fraser Mills Ltd.) and numerous energy companies operate in the area (e.g., Canadian Natural Resources Ltd., ConocoPhillips, Devon Canada Corporation, Encana Corporation, Suncor,

Transcanada Pipelines Ltd., Talisman Energy Inc., Husky Energy, and BP Canada). Current estimates of the industrial footprint indicate approximately 62 km of major roads (>15m), 1491 km of minor roads (>8m), 1065 km of pipelines, 8640 km of seismic lines, 692 ha covered by wellsites and 25,844 ha of cutblocks created over the past 30 years (WCCLPT 2008). Overall, 88% of the LSM range is less than 250m from anthropogenic features, above the 61% threshold to ensure sustainable caribou populations (Sorensen et al. 2008).

Intense management efforts were put in place in 2005-2006 to help recover the LSM caribou population. The Fish and Wildlife Division of Alberta Sustainable Resource Development (ASRD) implemented wolf control within the caribou range: 104 wolves were removed in the 2005-2006 winter, 66 wolves were removed the following winter, 72 wolves were removed in the 2007-2008 winter, and 120 were killed in 2008-2009 (D. Hervieux, ASRD, unpublished data). Wolves were removed mostly by aerial gunning from helicopters, although strychnine poisoning was also used to kill wolves. In addition, populations of prey (moose, elk and deer) are being targeted for reductions through increased harvest limits that began in fall 2006. Permits for harvest of antlerless moose and elk were issued in target WMUs and the white-tailed deer (*O. virginianus*) harvest limit number was raised to three. Further, ASRD implemented the LSM caribou calf pilot project where calving caribou were penned in March 2006 to decrease calf losses to predation. This project was discontinued because calf survival of penned caribou did not differ from other calves, suggesting that the wolf-control

program had successfully decreased predation on calves (ASRD, unpublished report).

THESIS OVERVIEW AND OBJECTIVES

My research project began in September 2006 when it was apparent that adequate monitoring was not in place to examine the effects of intensive management actions aimed at rescuing the Little Smoky caribou herd. Although the current provincial management strategy is one of adaptive management, it is difficult to know the consequences of management actions when sufficient monitoring is not in place. The goal of this thesis is to address two issues related to current management strategies in the Little Smoky:

1) After wolf removal, non-wolf predators could negatively affect calf survival and recruitment.

Although wolves are believed to be the caribou's main predator, a number of other predators are present in the LSM including grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Puma concolor*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*) and coyotes (*C. latrans*) (Smith 2004). Removal of wolves raises concern over changes in predator-prey dynamics that might allow other predators to compensate for reduced wolf predation, particularly on caribou calves (Gasaway et al. 1992). Prior to wolf control (2001–2005) average adult female survival in the LSM was estimated at 83% but average calf recruitment was only 12 calves per 100 females (ACC 2008). Improved calf recruitment is

thus a crucial component in the recovery of this caribou population. Even with wolf control, caribou recovery could be impeded if predation by other predators compensates for the reduction in calf predation by wolves.

Bear predation on ungulates has been reported in many regions. During the 2006 LSM caribou calf penning program calves born in pens were all fitted with radiocollars. Several calves were lost and in two of the three cases where calf remains were observed, bear predation was the most likely cause of mortality (ASRD, unpublished report). Recorded causes caribou mortalities in the LSM from 1984 to 2007 show that bear predation accounted for 16% of deaths (ACC, unpublished data). Bear predation has had important impacts on caribou survival in Quebec (Mosnier et al. 2008), Newfoundland, British Columbia (Ballard 1994), and Alaska (Young and McCabe 1997). Munro et al. (2006) found substantial amounts of ungulates (mostly moose) in grizzly bear diets in west-central Alberta, particularly in late spring. They also found that bears in the foothills area ate more ungulates than mountain bears. Zager and Beecham (2006) reviewed mortality of moose calves in North America finding that predation accounted for 2–50% (black bear) and 2–52% (grizzly bear) of mortalities. Significant bear predation on moose was also reported in east-central Alaska (Gassaway et al. 1992) and the southern Yukon (Larsen et al. 1989). Considerable elk predation by bears has been demonstrated in Yellowstone National Park (Barber-Meyer et al. 2008) and north-central Idaho (Onorato et al. 2006).

Bears clearly have the potential to play a significant role in the survival and persistence of caribou because they might be acting as a limiting factor for certain

populations. Gasaway et al. (1992) suggested that grizzly bear predation on moose might have compensated for the decline in wolf predation in a treatment area where 77.6% of wolves were removed but no change in cow to calf ratios were observed. Further, Ballard (1994) concluded that the black bear's role as a potential limiting factor for caribou depends on bear density in relation to other predator densities and prey numbers. Because the role of bears in caribou ecology is not well understood in the LSM, performing a bear diet analysis to quantify the importance of caribou in bear diets is an important first step in understanding their role in caribou survival.

In Chapter 2, I test the application of stable isotope analysis to identify the importance of bears (*U. arctos* and *U. americanus*) in calf survival by reconstructing bear diets. I collected grizzly and black bear hair samples across the LSM study area (Figure 1–3) from barbed-wire bait stations. Diet reconstruction was performed by comparing ratios of heavy isotopes (^{13}C and ^{15}N) in bear hair to those found in a variety of potential bear foods. My objective was to document the relative importance of caribou in bear diets after wolf abundance has been significantly reduced. Although there was no evidence that bears were killing caribou, I found wide variation in diet among individual bears in the population.

2) Controversy surrounding aerial gunning and poisoning of wolves.

Predator-control programs often elicit strong public reactions, either positive or negative. The use of aerial gunning and poisoning to remove wolves has in the past met considerable public opposition (NRC 1997, Dekker 2007). In Chapter 3,

I examine the spatial and temporal patterns of wolf harvest on registered traplines across Alberta from 1985 to 2006. My objectives were to understand the impact trappers have on the provincial wolf population and to evaluate the role of trapping in wolf management.

I conclude the thesis with chapter 4 where I summarize my findings in a public-interest article for the *Alberta Outdoorsmen* that links the current situation in the LSM to the information I gathered on predators and predator management.

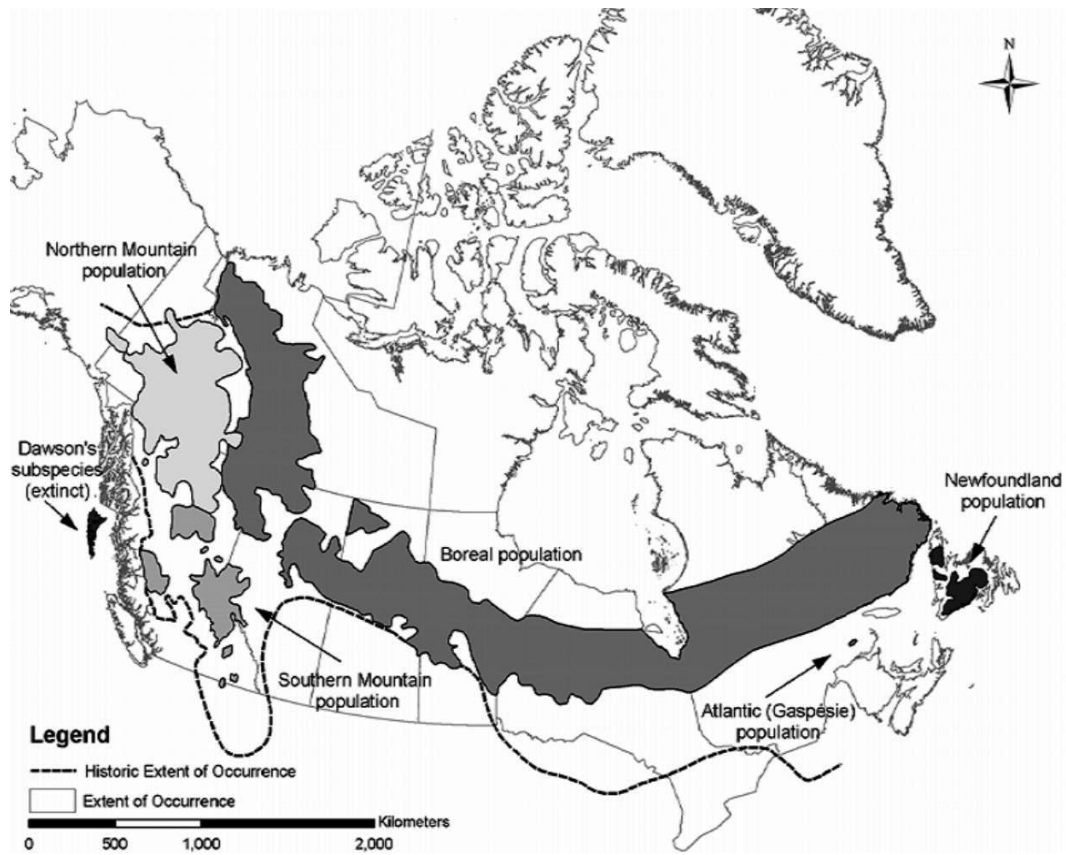


Figure 1–1. Current and historic extent of forest-dwelling woodland caribou in North America in 2001(modified from Thomas and Gray 2002).

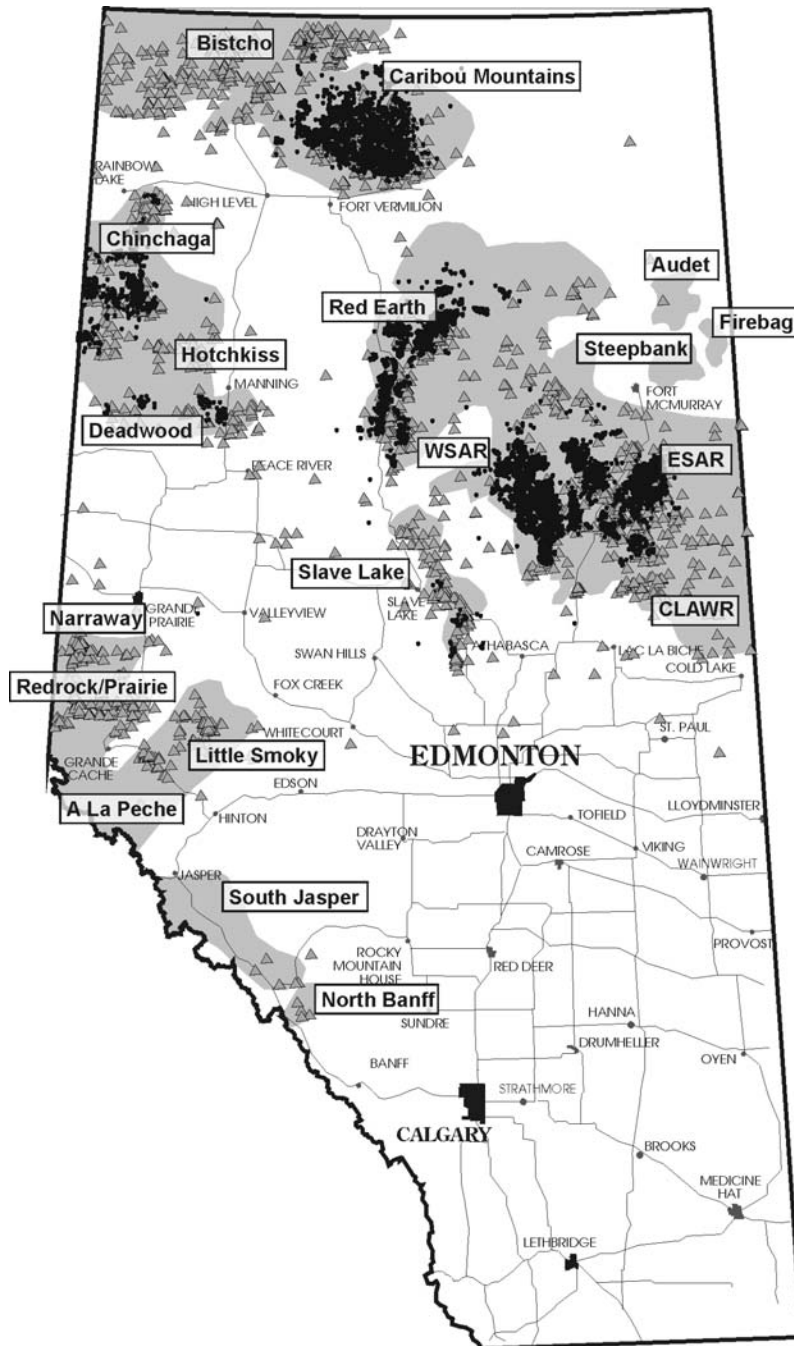


Figure 1–2. Location and names of woodland caribou herds in Alberta (from Dzus 2001). The Narraway, Redrock Prairie Creek, A la Peche, South Jasper and Banff herds are classified as mountain ecotype and all other herds are boreal populations. Dots represent telemetry locations and triangles are a combination of incidental sightings and local knowledge.

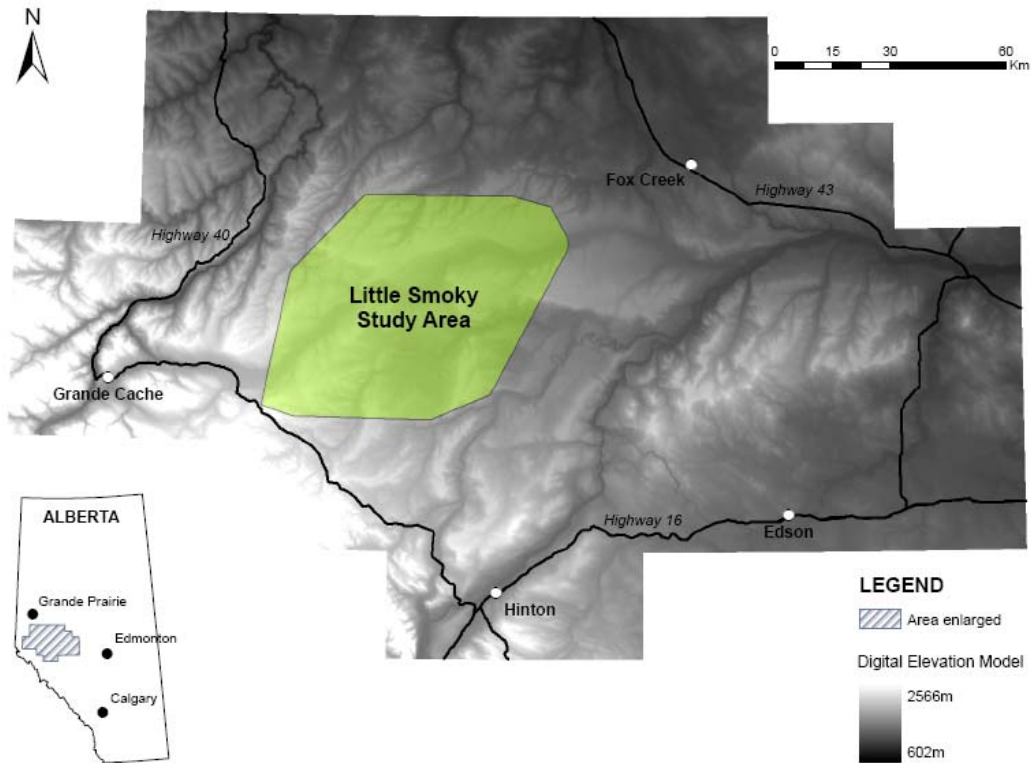


Figure 1–3. Study area in west-central Alberta encompassing the Little Smoky woodland caribou range.

LITERATURE CITED

- Alberta Caribou Committee (ACC). 2008. Annual statistics for provincial caribou herds (2003-2004 to 2007-2008). www.albertacariboucommittee.ca (accessed November 2008).
- Alberta Sustainable Resource Development (ASRD). 2007. Little Smoky Caribou Calf Penning Program – Evaluation to September 2006. Fish and Wildlife Division, Unpublished report.
- Anderson, R. B. 1999. Peatland habitat use and selection by woodland caribou (*Rangifer tarandus caribou*) in northern Alberta. M.Sc. thesis, University of Alberta, Edmonton, AB.
- Alberta Woodland Caribou Recovery Team. 2005. Alberta woodland caribou recovery plan 2004/05-2013/14. Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Recovery Plan No. 4. Edmonton, AB.
- Ballard, W. B. 1994. Effects of black bear predation on caribou- a review. *Alces* 30: 25–35.
- Ballard, W. B., P. R. Krausman, S. Boe, S. Cunningham, and H. A. Whitlaw. 2000. Short-term response of gray wolves, *Canis lupus*, to wildfire in northwestern Alaska. *Canadian Field-Naturalist* 114: 241–247.
- Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* 169: 1–30.
- Bergerud, A. T. 1974. Decline of caribou in North America following settlement. *Journal of Wildlife Management* 38: 757–770.

- 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.
- Bergerud, A. T. and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64: 1515–1529.
- Bergerud, A. T. and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as an antipredator tactic. *Canadian Journal of Zoology* 65: 1597–1606.
- Bradshaw, C. J., D. M. Hebert, A. B. Rippin, and S. Boutin. 1995. Winter peatland habitat selection by woodland caribou in north-eastern Alberta. *Canadian Journal of Zoology* 73: 1567–1574.
- Bradshaw, C. J. A., S. Boutin, and D. M. Hebert. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. *Journal of Wildlife Management* 61: 1127–1133.
- Courtois, R., J. P. Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use and mortality of woodland caribou. *Écoscience* 14: 491–498
- Dalerum, F., S. Boutin, and J. S. Dunford. 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. *Canadian Journal of Zoology* 85: 26–32.
- Dekker, D. 2007. An historical perspective on Alberta's current wolf wars. *Nature Alberta* 36: 12–13.
- De Vos, A., and R. L. Peterson. 1951. A review of the status of woodland caribou

- (*Rangifer caribou*) in Ontario. *Journal of Mammalogy* 32: 329–337.
- Dunford, J. S., D. P. McLoughlin, F. Dalerum, and S. Boutin. 2006. Lichen abundance in the peatlands of northern Alberta: Implications for boreal caribou. *Écoscience* 13: 469–474.
- Dyer, S. J., J. P. O'Neil, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management* 65: 531–542.
- Dyer, S. J., J. P. O'Neil, S. M. Wasel, and S. Boutin. 2002. Quantifying the effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology* 80: 839–845.
- Dzus, E. 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 30, Edmonton, AB.
- Edmonds, E. J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. *Canadian Journal of Zoology* 66: 817–826.
- Edmonds E. J., and M. I. Bloomfield. 1984. A study of woodland caribou (*Rangifer tarandus caribou*) in west-central Alberta, 1979–1983. Unpublished report, Alberta Energy and Natural Resources, Fish and Wildlife Division, Edmonton. AB.
- Edmonds, E. J., and K. G. Smith. 1991. Mountain caribou calf production and

survival, and calving and summer habitat use in west-central Alberta.

Wildlife Research

Series No. 4, Alberta Fish and Wildlife Division, Edmonton, AB.

Edwards, R. Y. 1954. Fire and the decline of a mountain caribou herd. *Journal of Wildlife Management* 18: 521–526.

Environment Canada. 2008. Scientific review for the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. August 2008. Ottawa, Ontario, Canada.

Fuller T. K., and L. B. Keith. 1981. Woodland caribou population dynamics in northeastern Alberta. *Journal of Wildlife Management* 45: 197–213.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kellyhouse, R. O. Stephensen, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs*.
120: 1–59.

Gustine, D. D, K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs* 165: 1–32.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12: 197–229.

Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. *Annual Reviews in Ecology and Systematics* 25: 495–520.

- 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, AB.
- James, A. R. C., and A. K. Stuart-Smith. 2000. Distribution of Caribou and Wolves in Relation to Linear Corridors. *Journal of Wildlife Management* 64: 154–159.
- James, A. R. C., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and it's relation to predation by wolves. *Journal of Wildlife Management* 68: 799–809.
- Johnson, D. R. 1985. Man-caused deaths of mountain caribou, *Rangifer tarandus*, in southeastern British Columbia. *Canadian Field Naturalist* 99:542–544.
- Klein, D. R. 1971. Reaction of Reindeer to Obstructions and Disturbances. *Science* 73: 393–398.
- Larsen, C. P. S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *Journal of Biogeography* 24: 663–673.
- Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in the southwest Yukon. *Journal of Wildlife Management* 53: 548–557.
- McLoughlin, P. D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in Populations of Woodland Caribou. *Journal of Wildlife Management* 67: 755–761.
- Mosnier, A., D. Boisjoly, R. Courtois, and J. P. Ouellet. 2008. Extensive predator

- use can limit the efficacy of a control program. *Journal of Wildlife Management* 72: 483–491.
- Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy* 87: 1112–1121.
- National Research Council (NRC). 1997. Wolves, bears, and their prey in Alaska: Biological and social challenges in wildlife management. National Academy Press, Washington, D.C., USA.
- Onorato, D., C. White, P. Zager, and L. P. Waits. 2006. Detection of predator presence at elk mortality sites using mtDNA analysis of hair and scat samples. *Wildlife Society Bulletin* 34: 815–820.
- Rempel, R. S., P. C. Elkie, A. R. Rodgers, and M. J. Gluck. 1997. Timber management and natural-disturbance effects on moose habitat: landscape evaluation. *Journal of Wildlife Management* 61: 517–524.
- Rettie, W. J., and F. Messier. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology* 76: 251–259.
- Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildlife Monographs* 113: 1–58.
- Seip, D. R. 1992. Factor limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70: 1494–1503.

- Smith, K. G. 2004. Woodland caribou demography and persistence relative to landscape change in west-central Alberta. M.Sc. thesis, University of Alberta, Edmonton, AB.
- Smith, K. G., E. J. Ficht, D. Hobson, T. C. Sorensen, and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. *Canadian Journal of Zoology* 78: 1433–1440.
- Sorensen, T., P. D. McLoughlin, D. Hervieux, E. Dzus, J. Nolan, B. Wynes, and S. Boutin. 2008. Determining sustainable levels of cumulative effects for boreal caribou. *Journal of Wildlife Management* 72: 900–905.
- Stuart-Smith, A. K., C. J. A. Bradshaw, S. Boutin, D. M. Hebert, and A. B. Rippin. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. *Journal of Wildlife Management* 61: 622–633.
- Thomas, D. C., and D. R. Gray. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada, in COSEWIC assessment and update status report on the Woodland Caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, ON.
- Vistnes, I., and C. Nellemann. 2007. The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biology* 31: 399–407.
- Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. *Global Change Biology* (in press).
- West Central Caribou Landscape Planning Team (WCCLPT). 2008. West Central

Caribou Landscape Plan. Submitted to the Alberta Caribou Committee.

- 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.
- Wittmer, H. U., B. N. McLellan, R. Serrouya, and C. D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology* 76: 568–579.
- Young, D. D., and T. R. McCabe. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. *Journal of Wildlife Management* 61: 1056–1066.
- Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators of ungulates in North America. *Ursus* 17: 95–108.

CHAPTER 2: INDIVIDUAL DIET VARIATION IN BEARS BASED ON STABLE-ISOTOPE METHODS IN WEST-CENTRAL ALBERTA

INTRODUCTION

Black bear (*Ursus americanus*) and grizzly bear (*U. arctos*) are often described as opportunistic generalists known to feed on vegetation, fruit, nuts, fish, terrestrial meat, and insects (Pasitschniak-Arts 1993, Lariviere 2001). Bear diets vary geographically depending on food availability (Hilderbrand et al. 1999a, Mowat and Heard 2006) and certain populations specialize on particular resources. For example, coastal populations have access to spawning salmon and therefore consume large quantities of fish whereas inland populations tend to rely more heavily on vegetation, berries and terrestrial meat (Hilderbrand et al. 1996, Hilderbrand et al. 1999a, Mowat and Heard 2006). Some grizzly bears feed extensively on army cutworm moths (*Euxoa auxiliaris*) by excavating the insects from aggregate sites on alpine talus slopes (Mattson et al. 1991, White et al. 1998, White et al. 1999). In the central Canadian Arctic, grizzly bears tend to be carnivorous with barren ground caribou (*Rangifer tarandus*) making up the majority of bear diets in spring and fall (Gau et al. 2002). In Yellowstone National Park most grizzly bears make extensive use of whitebark pine (*Pinus albicaulis*) nuts during years of good cone production (Mattson and Reinhart 1997, Felicetti et al. 2003).

Bears have the ability to develop foraging specializations as demonstrated by dietary differences across geographical areas; however, few studies have

examined dietary variation within bear populations. Bear dietary studies generally have focused on describing average population diet and nutritional differences among populations (e.g., Hilderbrand et al. 1999, Mowat and Heard 2006, Munro et al. 2006) or between sympatric species (e.g., Jacoby et al. 1999, Hobson et al. 2000, Belant et al. 2006, Fortin et al. 2007). A growing number of studies are documenting the occurrence of individual specialization within populations which has been reported in taxa ranging from invertebrates to mammals (Bolnick et al. 2003). Individual dietary specialization is of interest to biologists because specialization can have important ecological, evolutionary, and conservation implications (Bolnick et al. 2003, Estes et al. 2003, Urton and Hobson 2005, Bolnick et al. 2007). For example, individual variation is a strategy that can be used by omnivores to partition resources in an environment. This approach takes advantage of the efficiency of learning how to exploit a subset of resources in a heterogeneous environment to decrease intraspecific competition (Bolnick et al. 2003) thereby increasing carrying capacity.

I set out to examine dietary variation within populations of black and grizzly bears in west-central Alberta. This location was selected because of intensive management efforts put in place to recover the nearly extirpated Little Smoky (LSM) woodland caribou herd. Recovery efforts include an on-going wolf-control program which could be compromised if bears compensate to prey on caribou in the absence of wolves. I used carbon (^{13}C) and nitrogen (^{15}N) stable isotope analysis to reconstruct black bear and grizzly bear diets in the LSM. The goals of this chapter are to use non-invasive stable isotope methods to (1) describe

bear diets in the LSM area, (2) evaluate potential for identifying caribou in bear diets, and (3) examine dietary variation among individuals.

Stable isotope techniques have been used in a variety of ecological studies (Hobson and Wassenaar 1999) including use by field ecologists to quantify animal diets (e.g. Hilderbrand et al. 1996, Thompson et al. 2005). The approach is based on the principle that naturally occurring stable-isotope ratios in a consumer's tissue can be related to those in its diet (DeNiro and Epstein 1978). Stable-isotope ratios of metabolically inactive tissues such as hair and nails are reliable indicators of consumption over the period of tissue growth (Hobson 1999). A number of studies have described advantages of this approach over traditional dietary methods such as scat analysis (e.g., Jacoby et al. 1999, Hobson et al. 2000, Robbins et al. 2004). Stable isotope analysis has been used to study diets of diverse animal taxa from invertebrates to mammals (e.g., Hobson et al. 1994, Ben-David et al. 1997, Ostrum et al. 1997, Cree et al. 1999, Vander Zanden and Vadeboncoeur 2002) and the technique has been applied to study the nutritional ecology of bears (e.g., Hilderbrand et al. 1996 and 1999, Jacoby et al. 1999, Hobson 2000, and Mowat and Heard 2006).

Isotopic ratios are measured using the delta (δ) notation, meaning that results are reported in parts per thousand (‰) as ratios relative to standards of either PeeDee Belmite (carbon) or atmospheric nitrogen (nitrogen) as follows:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where δX is $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ and R is the $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratio (Peterson and Fry 1987, Kelly 2000). Ratios of nitrogen ($\delta^{15}\text{N}$) generally show an enrichment of 2–5‰ between each trophic level and therefore are indicative of trophic position (DeNiro and Epstein 1981, Minagawa and Wada 1984, Bocherens and Drucker 2003). Carbon stable isotopes ($\delta^{13}\text{C}$) do not vary much as they move through food webs, but $\delta^{13}\text{C}$ values can differ between sources (e.g., terrestrial versus marine). Carbon isotopes then can provide useful information on relative use of different dietary carbon sources (Tiezan et al. 1983, Peterson and Fry 1987). The combined use of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can yield information on both trophic level and source of dietary inputs.

STUDY AREA

This study was conducted within the LSM caribou range located in the foothills of west-central Alberta (Figure 2–1). The area includes both upper and lower foothills natural subregions, which are predominately covered by forest (Natural Regions Committee 2006). The upper foothills are characterized by conifer-dominated forests of lodgepole pine (*Pinus contorta*), black spruce (*Picea mariana*) and some white spruce (*Picea glauca*) whereas the lower foothills are typically mixedwood forests with aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), lodgepole pine, black spruce, white spruce, balsam fir (*Abies balsamea*) and tamarack (*Larix laricina*) present in different areas (Natural Regions Committee 2006). Both subregions have a mix of upland and lowland habitats. Shrubby grasslands with willow

(*Salix* spp.), shrub birch (*Betula* spp.), and some aspen occur at the driest sites along drainages and black spruce and tamarack-dominated bogs, fens, and muskegs occur in wetter lowland sites (Smith et al. 2000). The climate is characterized by long, cold, dry winters and short, cool, wet summers (Smith et al. 2000).

Major land uses include logging and oil and gas exploration and development which has resulted in a significant industrial footprint resulting from over 30 years of activity from the forestry and energy sectors (see Chapter 1). Recreational land-uses include hiking, camping, fishing, off-road vehicle use (snowmobiles and all-terrain vehicles), hunting, and trapping. Access was available on all-weather and dry-weather resource roads, or along seismic lines, pipelines and powerlines (Smith et al. 2000).

METHODS

Sample collection

I collected hair samples from black and grizzly bears using hair-snag techniques developed by Woods et al. (1999). Protocol was approved by the University of Alberta's Biosciences Animal Policy & Welfare Committee (Protocol #545707). Bait stations consisted of a single strand of barbed-wire wrapped around 3–6 trees (approximately 50cm above ground) with a beaver carcass suspended in a burlap sack from a central tree (2–3 m above ground). I dispersed stations across the Little Smoky caribou range according to black bear home range size to get a representative sample of the black bear population although some grizzly bear

samples were anticipated. Black bear home range estimates in Alberta are highly variable. Mean home range sizes for black bears in the Cold Lake area of NE Alberta were 119 km² (range: 42–196 km²) and 19.6 km² (range: 3–63 km²) for males and females respectively (Young and Ruff 1982). In east-central Alberta Czetwertynski et al. (2007) reported average home range sizes of 58 km² (range: 21–233 km²) and 27.5 km² (range: 15–63 km²) for hunted and unhunted females respectively, and 378 km² (range: 269–686 km²) and 123.5 km² (range: 90–245 km²) for hunted and unhunted males. I created a grid of 10×10 km cells over the LSM caribou range (as defined by caribou home ranges mapped by Neufeld (2006)) and attempted to set 2 hair-snag enclosures within those grid cells that were completely covered by caribou home ranges, and only 1 station if the grid was only partially covered by caribou home range. I chose this particular design to obtain a bait station density of approximately one station per 50 km². Enclosures were placed at least 5 km apart from each other and site selection was based on accessibility and habitat features (proximity to game trail, proximity to water, and vegetation cover).

I baited enclosures in mid July 2007 and revisited each 4 times at 7–10 day intervals. Hair samples were stored in paper envelopes and enclosures were sprayed with beaver castor after each visit. If several hair samples were collected from the same bait station during the same sampling event they were assumed to belong to a single bear, but samples were kept separate. The isotopic signatures I report are then the means of all samples collected at one station. This decision was based on the assumption that bears usually are solitary, with the exception a

mother travelling with her cubs (Pelton 2000, Lariviere 2001) or males associating with females during breeding season in June. In the case of a mother and cubs the resulting isotopic ratios would likely be indistinguishable because the family unit would be feeding on the same foods, and treating them as individuals would artificially increase the estimated minimum number of ungulates eaten by bears.

I opportunistically collected plant samples within the study area during the spring and summer of 2008 based on a compiled list of potential bear foods (Holcroft and Herrero 1991, Lariviere 2001, Pelton 2000, Munro et al. 2006). Samples were placed in Ziploc bags and stored in a portable cooler until they could be frozen. I collected ants (Formicidae) from various locations within the study area. Ungulate samples were provided by Alberta Fish and Wildlife officers who collected hair and muscle tissue from road-killed animals and 25 caribou hair samples were provided by Fiona Schmiegelow (collected during captures in March 2003 and February 2005). I conducted three fixed-wing telemetry surveys (May 12th, June 2nd, June 25th) to locate any dead radiocollared caribou, which would later be visited on the ground to collect tissue samples (muscle or hair). Two additional telemetry flights were completed by helicopter as part of Alberta Fish and Wildlife Division's caribou calf surveys (May 26th and June 19th). All aerial surveys were conducted during and shortly after calving season to increase chances of finding and obtaining samples from calves. Non-caribou ungulate samples were supplemented using isotopic values reported in the literature. I created a caribou calf isotopic signature by supplementing samples

with adjusted adult caribou samples. I added +1.9‰ to adult nitrogen values to reflect the nitrogen enrichment observed in young calves (Jenkins et al. 2001).

Sample Preparation and Isotopic Measurements

I identified hair as black or grizzly according to Mowat and Strobeck (2000) and rinsed samples twice with a 2:1 chloroform: methanol solution before letting them dry under a fume hood (Urton and Hobson 2005). I homogenized samples by cutting hair in small pieces with scissors and then loaded sub-samples of 1.5–2.8 mg into 5×9 mm tin cups (Isomass Scientific). Isotopic analysis was completed with a Model 440 Elemental Analyzer (Control Equipment Corporation) at the biogeochemical lab, University of Alberta. Analytical error was estimated at ±0.1‰ for carbon and ±0.2‰ for nitrogen.

I dried plant samples in a drying oven for 1 week, ground them using a ball grinder, and loaded sub-samples of the powdered material in 3×5 mm tin cups (weights varied depending on species). I freeze-dried muscle tissue and whole ant samples in glass scintillation vials, ground them using a hand grinder and loaded sub-samples of approximately 1.0 mg of powdered tissue into 3×5 mm tin cups. Plant and animal tissue samples were submitted for analysis at the University of Saskatchewan Isotope Laboratory. Analysis was performed using a Thermo Finnigan Flash 1112 Elemental Analyzer with an analytical error of ±0.1‰ for carbon and ±0.4‰ for nitrogen.

I used a k-means cluster analysis performed in STATA SE 10.0 (StataCorp, College Station, Texas) to identify bear groups of similar isotopic signatures.

Bear Landscape Use

In a geographical information system (GIS) I created a north-south line bisecting the range in 2 approximately equal areas. For the north south comparison I used the Little Smoky River as the bisection line. I examined coarse-scale use of the landscape by bears using t-tests to compare the average number of bear visits observed between east and west sides of the caribou range as well as between north and south sides. Statistical analysis was performed using STATA SE 10.0 (StataCorp, College Station, Texas).

Diet composition

Simple linear mixing models can determine a unique mathematical solution for the diet of a consumer when $n + 1$ isotopically distinct food sources are used with n stable isotopes (Phillips 2001). In my case, the number of distinct dietary inputs ($n = 7$) exceeded the number of isotopes used in the analysis ($n = 2$). I therefore used a multiple-source mixing model (Isosource 1.3, U.S. Environmental Protection Agency, Corvallis Oregon) to determine the relative contributions of potential food items in bear diets. I used a K nearest-neighbour randomization test to ensure statistical difference between food groups I created (Rosing et al. 1998) and followed methods outlined by Phillips et al. (2005) to group food sources into categories. The 7 food groups used were caribou, caribou calf, ants, ungulates (combination of mule deer, white-tailed deer, elk and moose), low-nitrogen plants ($\leq -3.0\text{‰}$), medium-nitrogen plants ($> -3.0\text{‰}$ to 4.0‰), and high-nitrogen plants ($> 4.0\text{‰}$). The multiple-source mixing model approach does not offer a unique solution because Isosource uses an iterative approach to find all

possible solutions that satisfy the principle of mass balance. The inputs to this model include isotopic values of consumer tissues, isotopic values of food sources (corrected with the appropriate fractionation values), the mass balance tolerance value permitted about the consumer's isotopic signature, and the interval increment used in the iterative procedure.

Isotopic fractionation can be defined as the change in heavy isotope ratio that occurs between a consumer's diet and its tissues (Fry 2006), and fractionation values can vary between different tissue types (Hilderbrand et al. 1996). The process arises from various enzymatic steps subsequent to the ingestion of food because similar molecules of slightly different masses (i.e., heavy versus light isotopes) react at different rates (Peterson and Fry 1987). Food sources must then be corrected to account for the isotopic enrichment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ that occurs between digestion and assimilation of food. Fractionation values are determined by feeding trials, and a few studies have examined diet-tissue discrimination values for bears (e.g. Hilderbrand et al. 1996, Felicetti et al. 2003). Fractionation values used for bears have ranged from +0.4‰ to +4.5‰ for $\delta^{13}\text{C}$ and +3.0‰ to +5.0‰ for $\delta^{15}\text{N}$ (Hilderbrand et al. 1996, Jacoby et al. 1999, Felicetti et al. 2003, Ben David et al. 2004, Mowat and Heard 2006). I chose to correct food sources by +2.6‰ for $\delta^{13}\text{C}$ (DeNiro and Epstein 1978, Hilderbrand et al. 1996, Ben-David et al. 2004, Urton and Hobson 2005, Mowat and Heard 2006) and +4.0 ‰ for $\delta^{15}\text{N}$ (DeNiro and Epstein 1981, Hilderbrand et al. 1996, Jacoby et al. 1999, Felicetti et al. 2003). I corrected bear hair $\delta^{13}\text{C}$ by $-1‰$ to account for carbon

enrichment relative to other tissues (Ben David et al. 2004, Mowat and Heard 2006).

Mixing-models were estimated in Isosource with an increment value of 1% and a tolerance value of 0.1‰ (Phillips and Gregg 2003, Urton and Hobson 2005). All possible combinations of source contributions (0–100%) were then examined in 1% increments and feasible solutions were identified as those for which the mass balance summed to the observed isotopic mixture ($\pm 0.1\text{‰}$) of the consumer tissue. Phillips and Gregg (2003) recommended reporting the range of possible solutions (minimum to maximum proportion of each source) as opposed to the mean to avoid misrepresenting the results. Reporting the 1st–99th percentile as the range is ideal because the minimum to maximum span is sensitive to small numbers of observations on both tails of the distribution (Phillips and Gregg 2003). The range of possible solutions can be restricted even further by using non-isotopic constraints such as relative abundance of food sources, ease of capture, stomach or gut contents of the consumer, or relative nutritional quality (Phillips and Gregg 2003). I eliminated all solutions that had more assimilated caribou than ungulates based on the relative abundances of these animals and visual inspection of the mixing space diagram. Any source contribution with a mean $< 1\%$ was assumed to be absent from the diet (Mowat and Heard 2006).

To help interpret relative measures of assimilated meat obtained from mixing models, I performed calculations to convert relative proportions of food consumed into quantities (kg) based on bear energetic requirements. I performed these calculations for an average black bear weighing 100 kg. Daily energetic

intake was estimated by using the mid-point between maintenance cost and maximum intake rates from nutritional studies. Daily maintenance cost (not including reproduction and hibernation) was calculated as in Mattson (1997):

$$E_C = A_C (287 M^{0.712})$$

where E_C represents daily energetic cost in kJ day^{-1} , A_C is the activity cost factor, and M is body mass (kg). Activity cost factors range from 1.2 to 2.7 for large mammals (Robbins 1983) and I used an A_C of 2.7 for male bears (Mattson 1997).

Maximum intake rates vary depending on the type of food so I calculated these rates for fruit, meat, and vegetation and used the mean to represent the average maximum intake rate of a mixed diet. Maximum intake rate for fruit was determined using an equation developed by Welch et al. (1997):

$$I_F = (0.66) (M^{0.86})$$

where I_F is the maximum intake of fruit in kg. Maximum meat intake was estimated using an equation developed by Hilderbrand et al. (1999b):

$$I_M = 58.5M^{-0.37}$$

where I_M is the maximum intake of meat expressed as a percentage of body mass. Maximum vegetation intake was estimated using an equation developed by Rode et al. (2001):

$$I_V = 2.65 M^{0.44}$$

where I_V is the maximum intake of herbaceous vegetation in kg. All food masses were converted into kilojoules based on specific energetic content and digestibility (Table 2-1). Lastly, I converted whole ungulate (moose, elk, deer and caribou) weights into percentage of diet based on my estimate of a 100kg

bear's energy intake over 4 four months because hair samples collected represent assimilated diets from approximately May to August inclusively.

RESULTS

Sample collection

I set 45 barbed-wire enclosures surrounding baits across 2,491 km² of the study area, resulting in an average bait-station density of one per 55.4 km². The average nearest-neighbour distance between stations was 5.4 km. Twenty four stations (53%) were visited at least once by bears, and several stations were visited more than once (Figure 2–2). During my first visit to bait stations 13 enclosures had bear hair present and 16, 10, and 4 enclosures had bear hair present at the second third and fourth visits respectively. I collected 110 hair samples distributed among 43 separate sampling events (i.e., a sampling event is a single visit to a bait station). Only 9 samples were from grizzly bears and the rest were from black bears. I collected 57 plant samples and 4 ungulate samples.

Bear Landscape Use

No spatial patterns of bear landscape use were observed and there were no significant differences between the average number of bear visits at north and south station groupings ($t_{43} = -0.8488$, $P = 0.401$) or between east and west station groupings ($t_{43} = 0.2528$, $P = 0.802$). The absence of a pattern is consistent with my observation of bear activity across the entire caribou range.

Isotopic Measurements

Stable isotope analysis was performed on 90 bear hair samples (other samples did not have enough hair for analysis). Once results were pooled by sampling event I had 37 samples for which a mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were measured (Appendix A). As expected, most samples were from black bears ($n = 33$), and 5 were from grizzly bears. Grizzly bear and black bear isotopic signatures were comparable. Black bear isotope ratios ranged from -24.61‰ to -22.43‰ ($\delta^{13}\text{C}$), and from 2.20‰ to 5.65‰ ($\delta^{15}\text{N}$). Grizzly bear values ranged from -24.58‰ to -23.46‰ ($\delta^{13}\text{C}$), and 2.13‰ to 4.88‰ ($\delta^{15}\text{N}$) (Figure 2–3). Bears were divided into 3 clusters, which I classified as follows: mostly herbivorous, omnivorous, and more carnivorous (Figure 2–3).

Plant samples ($n = 57$) had $\delta^{13}\text{C}$ values ranging from -31.28‰ to -25.28‰ whereas $\delta^{15}\text{N}$ measurements showed more variability ranging from -6.28‰ to 7.73‰ (Appendix B). Caribou samples ($n = 27$) ranged from -25.40‰ to -22.54‰ ($\bar{x} = -24.48$) and 1.62‰ to 7.25‰ ($\bar{x} = 5.18$) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively. Isotope values for other ungulates were averages of samples collected in the field and values from the literature (deer: $n = 17$, $\bar{x}_{\delta^{13}\text{C}} = -25.66\text{‰}$, $\bar{x}_{\delta^{15}\text{N}} = 4.35\text{‰}$; elk: $n = 12$, $\bar{x}_{\delta^{13}\text{C}} = -25.59\text{‰}$, $\bar{x}_{\delta^{15}\text{N}} = 3.63\text{‰}$; moose: $n = 27$, $\bar{x}_{\delta^{13}\text{C}} = -25.81\text{‰}$, $\bar{x}_{\delta^{15}\text{N}} = 2.75\text{‰}$). All terrestrial meat values are included in Appendix C.

Diet Composition

The food groups used in Isosource all differed significantly ($P < 0.05$) with the exception of ungulates and ants ($P = 1.00$). Because the two foods are not related,

I did not group the values when calculating dietary contributions as suggested by Phillips et al. (2005).

Average isotope values used in the dietary mixing model resulted in the mixing space shown in Figure 2–4. Mean isotopic signature of bears is most similar to mid-level nitrogen plants. Although caribou and other ungulates differed in their isotope measurements, if eaten by bears they would have the same effect on the bear's isotope values because they occur along the same linear axis. The mixing space graph shows that caribou and other ungulates cannot be distinguished in bear diets and that there appears to be no caribou specialists among the bears sampled.

Despite not being able to distinguish caribou from other ungulates, I kept their values separate in Isosource. The model output gave all source contribution possibilities for each bear sample (Appendix D) but I pooled caribou, caribou calves, other ungulates, and ants into one category called terrestrial protein because these food groups could not be teased apart. Mean contributions of terrestrial protein ranged from 2.0% to 57.8%, low-nitrogen plants ranged from 6.1% to 48.7%, medium-nitrogen plants ranged from 2.5% to 72.5%, and high-nitrogen plants ranged from 1.2% to 13.7% (Figure 2–5). A species comparison of diet using average isotopic values of black bears and grizzly bears indicated that black bears assimilated more terrestrial protein than grizzly bears (Table 2–2).

I estimated a daily maintenance cost of 20,573.6 kJ for a 100kg black bear, and maximum daily intakes of $I_F = 51,903$ kJ, $I_M = 92,478$ kJ, and $I_V = 33,787$ kJ for fruit, meat and vegetation diets respectively. I estimated an average daily

energy intake of 40,029kJ. I converted whole ungulate weights of moose elk, deer and caribou into dietary contributions based on the bear's energetic intake over a four month assimilation period (Table 2–3).

DISCUSSION

Isotopic Measurements and Diet Composition

Measured values of carbon and nitrogen isotopes in bears ($\bar{x}_{\delta^{13}\text{C}} = -23.54$ and $\bar{x}_{\delta^{15}\text{N}} = 4.22$) were comparable to those reported in other studies, however, average $\delta^{15}\text{N}$ was at the lower end of the spectrum. In the central Saskatchewan boreal Urton and Hobson (2005) indicated average values of -22.7‰ and 6.4‰ for black bear $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively. Mowat and Heard (2006) reported average signatures for 5 Alberta grizzly bear populations ranging from -22.5‰ to -23.3‰ and from 4.2‰ to 5.5‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively. Differences in $\delta^{15}\text{N}$ may not necessarily reflect relative trophic position among populations as isotopic signatures vary across landscapes (Urton and Hobson 2005). Nitrogen ratios reflect local conditions so it may be more appropriate to compare assimilated dietary components which are calculated using local food sources.

Carbon isotope values had a narrow range (-24.61‰ to -22.43‰) presumably indicative of a single carbon source. Ratios of carbon isotopes do not vary much as they move through food webs, rather they tend to differ across sources such as between terrestrial, marine, or freshwater systems or between C_3 and C_4 plant sources (Rau 1978, Tiezan et al. 1983, Peterson and Fry 1987). I would expect LSM bears to exhibit a greater range in $\delta^{13}\text{C}$ if they had access to

more than one carbon source, such as spawning salmon (Jacoby et al. 1999, Darimont and Reimchen 2002).

Nitrogen isotope ratios generally show an enrichment of 2–5‰ between each trophic level therefore relative $\delta^{15}\text{N}$ values are indicative of trophic position (DeNiro and Epstein 1981, Minagawa and Wada 1984, Bocherens and Drucker 2003). I observed a large range of assimilated terrestrial protein in my samples (2–58%) resulting from a 3.45‰ range in $\delta^{15}\text{N}$ values. The variation in $\delta^{15}\text{N}$ values thus reflects individual variability in diets. I was unable to show specific inputs of caribou with any certainty but based on visual inspection of isotopic signatures it is obvious that none of the bears sampled were caribou specialists, which is not surprising given the scarcity of caribou in the study area.

The isotope method explored in this study failed to identify the relative importance of caribou in bear diets due to the confounding effect of other ungulate species. My approach however used only heavy isotopes of carbon and nitrogen, the most commonly used elements in isotope analyses. Using additional isotopes or exploring alternative methods such as mercury analysis, sodium flux or fatty acid analysis might enable the differentiation between meat sources (see Appendix E for more detail on these methods).

Interestingly, black bears assimilated more terrestrial protein than grizzly bears ($28 \pm 6\%$ and $19 \pm 5\%$ respectively). Based on previous studies of sympatric black and grizzly bear populations, I expected to observe larger amounts of terrestrial protein in grizzlies. Jacoby et al. (1999) studied sympatric brown and black bears on the Kenai Peninsula, Alaska and found that meat

(salmon and terrestrial meat) constituted 78% and 35% of brown and black bear diets respectively. In south-central Alaska, Belant et al. (2006) found substantial differences in mean assimilated dietary meat between sympatric black bears (27-30%) and brown bears (75-84%). Terrestrial animal matter comprised > 40% of grizzly bear spring diets in west-central Alberta (Munro et al. 2006) whereas black bears in southwestern Alberta had a maximum animal matter contribution of 17.3% (Holcroft and Herrero 1991). Hobson et al. (2000) however found a pattern similar to my study in the Upper Columbia River basin of British Columbia. Average contribution of meat in black bears was 10.2% (males = 8.3%, females = 15.0%) while sympatric grizzly bears averaged only 7.17% (males = 9.9%, females = 3.0%). Female grizzly bears did not appear to consume much meat which may reflect their use of high elevation habitats that have low abundance of large mammals (Hobson et al. 2000). Because sex and age of individuals I sampled is unknown, I cannot attribute lower assimilated terrestrial protein in grizzly bear diet to demographic differences.

Individual Variation in Diets

In this study I highlight the presence of large variation among diets of individual black bears. This appears to hold for grizzly bears although sample size was small. There are 2 potential explanations for the observed results: (1) bears with large terrestrial protein content are individual specialists that consume more meat, or (2) variation in terrestrial protein is a reflection of the large “package size” of meat (i.e., carcasses) which can create protein pulses in the assimilated diet.

Mechanisms leading populations of generalists to diversify into a series of specialists are not well understood. Three potential mechanisms have been suggested including spatial and/or temporal variation in food supply, phenotypic differences that affect foraging success, and frequency-dependent fitness benefits (Estes et al. 2003). The latter would have to operate with density-dependent effects because density-dependent depletion of resources drives intraspecific competition (Estes et al. 2003). In the case of bears, morphological differences are unlikely to contribute significantly to individual specialization, therefore differences are likely the result of behavioural factors. Bears maintain home ranges and therefore are territorial animals who have different resource availabilities depending on territory location. Territoriality in mammals has been linked with individual foraging specializations, for example grizzly bears with home ranges near streams ate significantly more fish than their neighbours (Mattson and Reinhart 1995). Angerbjorn et al. (1994) attributed greater marine food inputs in Arctic foxes to habitat heterogeneity and territoriality. Similarly, pine martens (*Martes americana*) with territories near trout-spawning streams consumed more fish than their neighbours (Ben David et al. 1997). Of course frequency-dependent effects also can play a role in developing foraging specializations because the benefit an individual gains from a particular resource depends on what other individuals in the population are doing (Estes et al. 2003). Even though certain foods have lower energetic value their benefits can equal those of higher quality foods when weighed against availability, ease of capture, the number of competitors, and predation risk. For example, female grizzly

bears with cubs reduced or avoided visits to salmon-spawning streams in the fall, even though salmon is a protein- and lipid-rich resource, due to the higher risk of infanticide in areas where bears congregate (Ben-David et al. 2004).

Social learning also could play a role in the development of foraging specialization in bears. Mazur and Seher (2008) demonstrated that food-conditioned foraging behaviour in black bears was transmitted through social learning. Black bear cubs reared in developed areas were 45 times more likely to be food-conditioned than cubs reared in the wild. Similarly, social learning appears to play an important role in shaping habitat selection strategies in grizzly bears (Nielsen 2005). Bear habitat selection could be predicted solely on learning experiences with no evidence of genetic contribution. In sea otters (*Enhydra lutris*) foraging specializations are shaped by social learning as pups learn to forage from their mothers (Estes et al. 2003).

According to the tangled bank hypothesis “biotic diversity is underlain and supported by environmental heterogeneity” (Bell 1982, Bell 1991). In other words resource partitioning has allowed a diversity of species to coexist and create complex biotic communities. We might then expect to observe dietary variation in generalist populations as a result of limited resources on the landscape. Individual specialization takes advantage of the efficiency of learning how to exploit a specific subset of resources in a heterogeneous environment to decrease intraspecific competition (Bolnick et al. 2003) and thereby increasing the landscape’s carrying capacity.

Alternatively, the observed variation in diets could be the result of bears consuming ungulate carcasses as they encounter them on the landscape. The energetic content of a single large carcass could be sufficient to provide a bear with a significant portion of its caloric requirement over the summer season depending on the ungulate species. A carcass could contribute anywhere between 1 to 52% of a 100 kg bear's energetic intake over a 4-month period. Of course this is assuming that the carcass is eaten entirely, an assumption that is unlikely to hold true due to losses to scavengers. In any case, a quarter of an average adult bull moose could still provide up to 13% of a bear's seasonal caloric requirement.

Regardless of the mechanism behind dietary variation, consuming more terrestrial protein is not without benefits and/or consequences. For example, increased amounts of salmon in grizzly bear diets was associated with larger body size, greater reproductive success, and higher population density (Hilderbrand et al. 1999b). Accordingly, we might expect that LSM bears with larger terrestrial protein intake would have superior body condition. Differences in diet can result in different exposure to predators and parasites which in turn can produce diet-specific risk factors (Durrell 2000, Bolnick et al. 2003). The timing of meat consumption also can influence the level of benefit gained by a bear, particularly in females. Meat eaten in the spring contributes to lean body mass gain whereas mass gain in the fall is mostly deposited as fat (Hilderbrand et al. 1999a). Fat deposition is more important in ensuring that the costs of hibernation and cub production are met (Elowe and Dodge 1989, Farley and Robbins 1995).

Large variation among individuals can have important implications for population dynamics modeling. Population models that incorporate individual variability can perform very differently (Łomnicki 1988) and have the added capacity for frequency-dependent events (Bolnick et al. 2003). For example, population viability analyses have not traditionally included individual heterogeneity but White (2000) demonstrated how the inclusion of this parameter improved viability estimates. The assumption that all individuals in a population have identical survival and reproductive parameters is flawed (White 2000) because variation in fitness can result from dietary differences among individuals (Bolnick et al. 2003, Urton and Hobson 2005). Łomnicki (1988) suggested that variability within a population can create greater population stability; however, typical deterministic models in ecology do not include individual variability thus omitting a potentially important source stability.

Conclusion

In this paper I described bear diets in the LSM area using non-invasive stable isotope techniques. Although the methods were not accurate enough to identify the relative amount of caribou in bear diets, I discovered very large variation in diets among individual bears even though the bears occurred in a relatively homogenous environment. I suggested 2 alternative explanations for this variation (1) bears with large terrestrial protein content are individual specialists that consume more meat, or (2) variation in terrestrial protein is a reflection of the large package size of meat (i.e. carcasses) which can create protein pulses in the assimilated diet. Further work is required to tease these 2 mechanisms apart. Variation in assimilated terrestrial protein among individuals can result in differences in a number of characteristics such as body size and reproductive success. In addition, large dietary variation among individuals can have

important implications for population dynamics modeling such as population viability analyses.

Table 2-1. Nutritional details of 3 food sources used in bear energetics

calculations.

Food type	Energetic content (kJ g ⁻¹ dry weight)	Percent dry weight	Percent digestibility
Fruit	18.71 ^a	16.1 ^b	49.9 ^b
Meat	22.80 ^c	43.4 ^d	88.0 ^c
Herbaceous vegetation	18.28 ^e	15.5 ^a	59.5 ^f

^a From Pritchard and Robbins 1990^b Average from Welch et al. 1997^c From Mattson 1997^d Average from Mattson 1997 (adult moose, elk, mule deer) and Pritchard and Robbins 1990 (deer)^e Average from Pritchard and Robbins 1990 (clover, alfalfa, and tubers) and Golley 1961 (leaves, stems, branches, roots, and litter)^f Average from Rode et al. 2001

Table 2-2. Dietary contributions (mean \pm SD) for black bears and grizzly bears in the Little Smoky area.

Species	<i>n</i>	Dietary contribution (%)			
		Terrestrial protein	Low N plants	Medium N plants	High N plants
Black bear	33	28 \pm 6	33 \pm 8	29 \pm 12	10 \pm 8
Grizzly bear	5	19 \pm 5	31 \pm 7	42 \pm 10	8 \pm 7

Table 2-3. Proportions of energy from a 100 kg black bear's 4-month diet contained in whole ungulate carcasses.

Species	Live weight (kg) ^a	Edible dry weight (kg) ^a	Digestible energy (kJ) ^b	Percentage of diet
Moose				
Calf	180	55	110,335	22
Adult female	385	123	2,468,234	50
Adult male	446	143	2,869,573	58
Elk				
Adult female	233	76	1,525,088	22
Adult male	292	93	1,866,226	38
Mule deer				
Calf	21	3	60,201	1
> 8 months	34	4	80,268	2
Caribou				
Adult female	94	30	594,585	12
Adult male	121	39	774,488	16

^a Moose, elk, and mule deer from Mattson et al. 1997, caribou live weight from Parker 1981, caribou dry edible weight approximated based on average proportion of edible mass documented in moose, elk and mule deer.

^b Assuming digestive efficiency of 88%

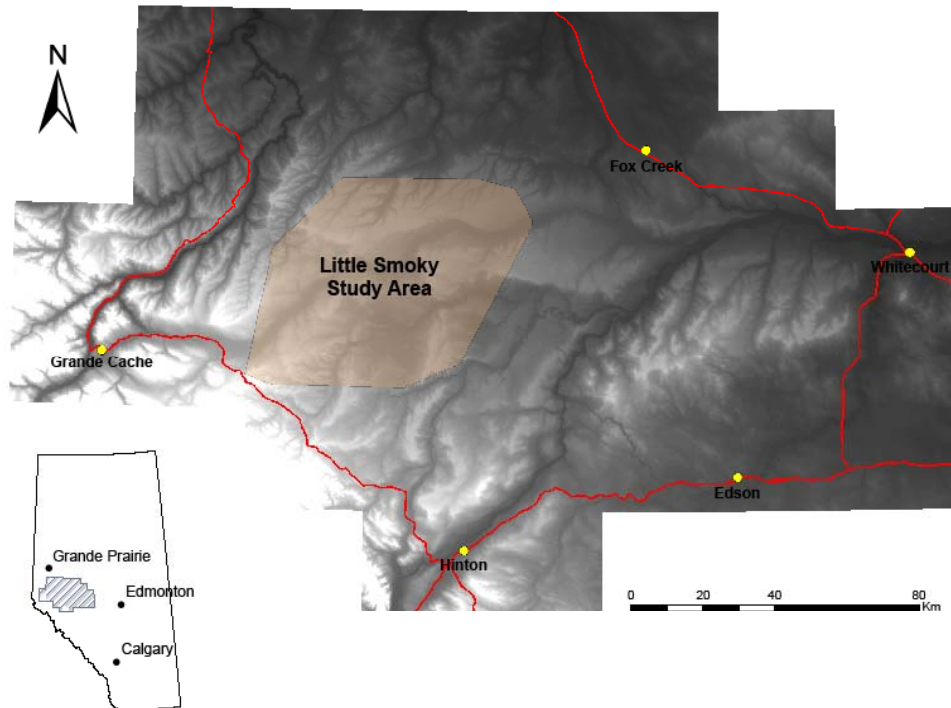


Figure 2–1. Map showing the Little Smoky study area in west-central Alberta.

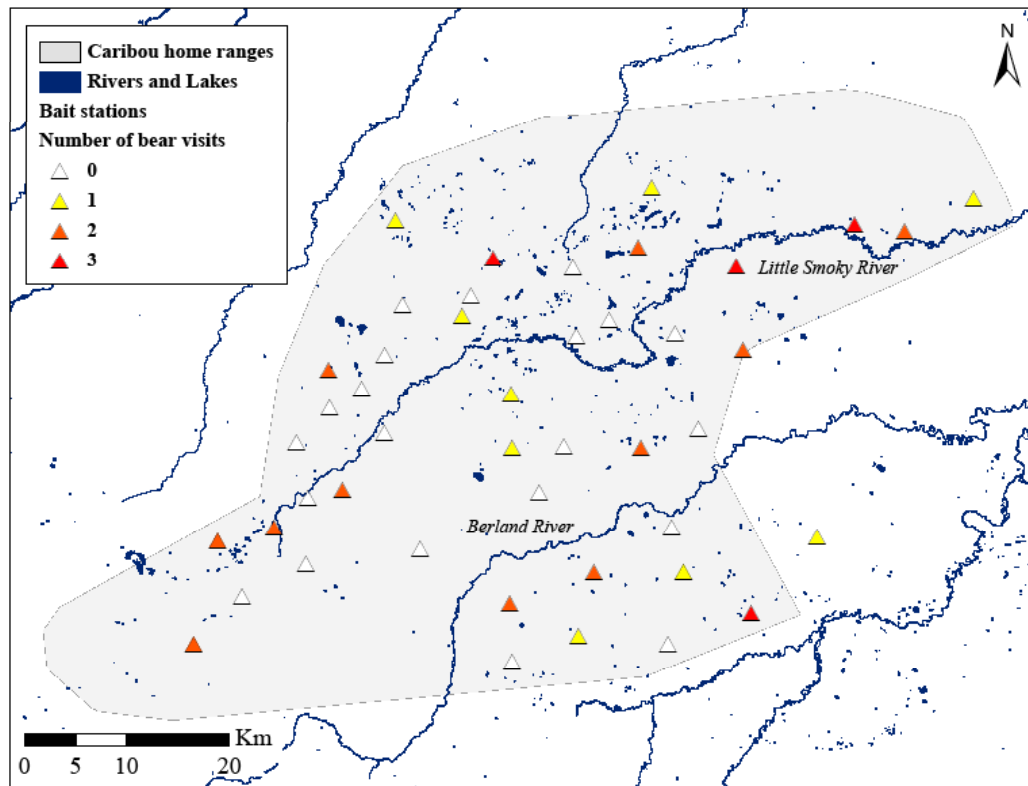


Figure 2–2. Bait station locations ($n = 45$) in the Little Smoky indicating the number time bear hair was collected over 4 repeated checks between July 13th to August 26th, 2007.

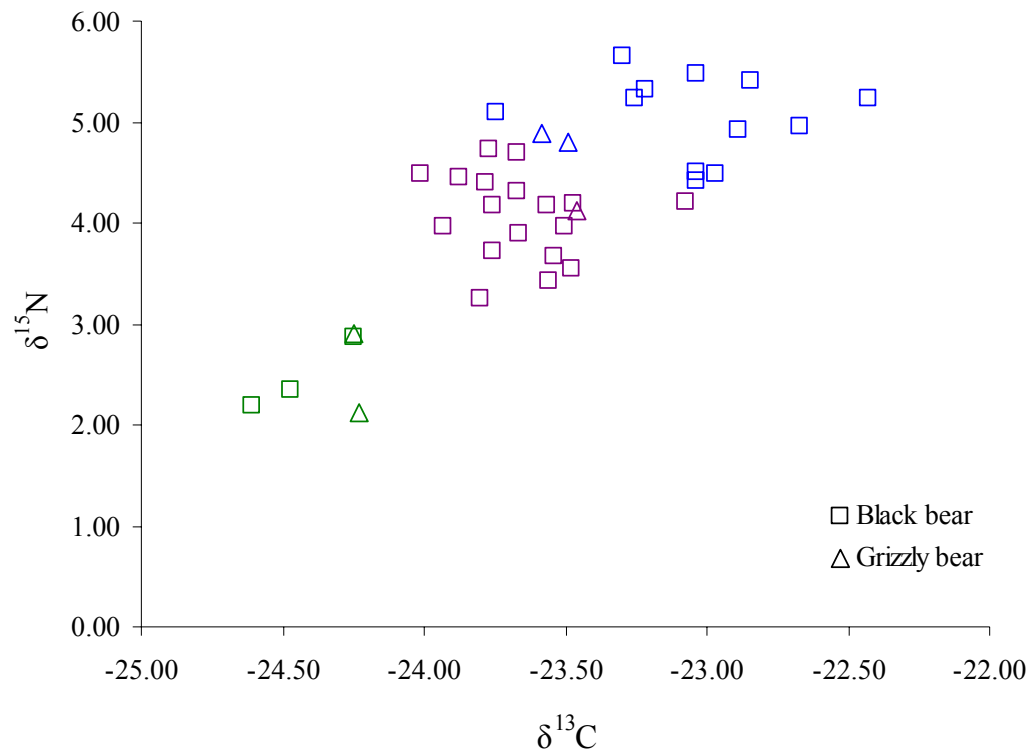


Figure 2–3. Ratios of heavy carbon and nitrogen isotopes in 38 bear hair samples collected in the Little Smoky caribou range. Open squares represent black bears, and triangles represent grizzly bears. Colours correspond to groups identified in a cluster analysis: mostly herbivorous (green), omnivorous (purple), and more carnivorous (blue).

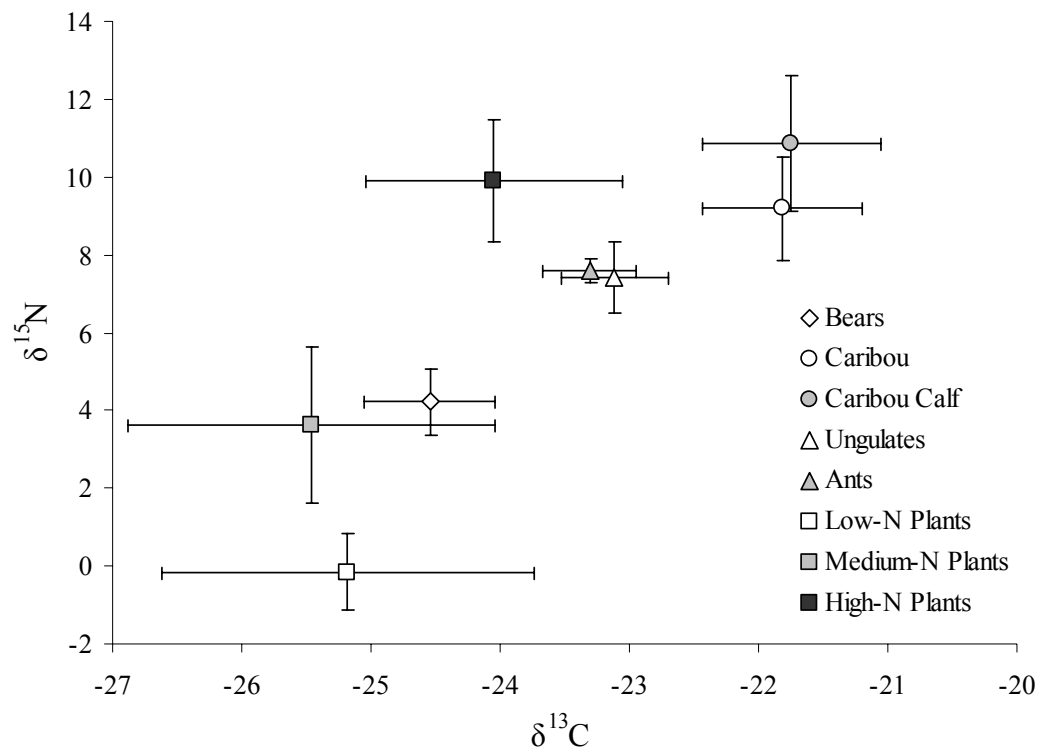


Figure 2–4. Mixing space diagram illustrating average (± 1 standard deviation) stable-isotope ratios of ^{13}C and ^{15}N for all food sources and mixture incorporated into the dietary mixing model. All values are corrected for fractionation.

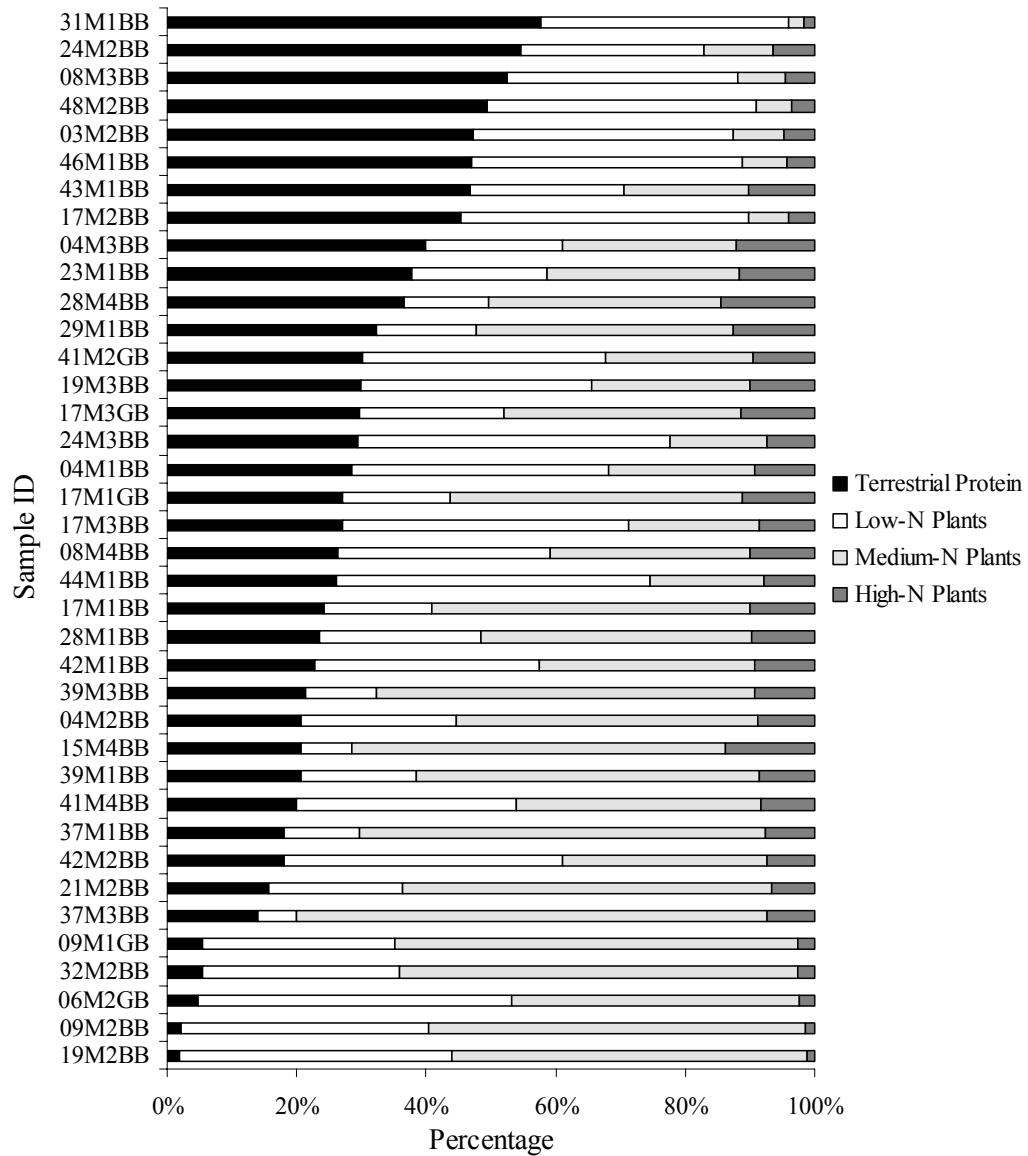


Figure 2-5. Mean contributions of four food groups in bear hair samples ($n = 38$) collected in the Little Smoky area.

LITERATURE CITED

- Angerbjorn, A., P. Herteinsson, K. Liden, and E. Nelson. 1994. Variation in Arctic foxes (*Alopex lagopus*): an analysis of stable carbon isotopes. *Oecologia* 99: 226–232.
- Belant, J. L., K. Kielland, E. H. Follman, and L. G. Adams. 2006. Interspecific resource partitioning in sympatric ursids. *Ecological Applications* 16: 2333–2343.
- Bell, G. 1982. *The masterpiece of nature: the evolution and genetics of sexuality*. University of California Press. Berkeley, California, USA.
- Bell, G. 1991. The ecology and genetics of fitness in *Chlamydomonas* III. genotype-by-environment interaction within strains. *Evolution* 45: 668–679.
- Ben-David, M., R. W. Flynn, and D. M. Schell. 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111: 280–291.
- Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138: 465–474.
- Bocherens, H., and D. Drucker. 2003. Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems. *International Journal of Osteoarchaeology* 13: 46–53.
- Bolnick, D. I., R. Svanbäck, M. S. Araújo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized

- populations also are more heterogeneous. *Proceedings of the National Academy of Science, USA*.104: 10075–10079.
- Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Husley, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161: 1–28.
- Cree, A., G. L. Lyon, L. Cartland-Shaw, and C. Tyrell. 1999. Stable carbon isotope ratios as indicators of marine versus terrestrial inputs to the diets of wild and captive tuatara (*Sphenodon punctatus*). *New Zealand Journal of Zoology* 26: 243–253.
- Czetwertynski, S. M., M. S. Boyce, and F. K. Schmiegelow. 2007. Effects of hunting on demographic parameters of American black bears. *Ursus* 18: 1–18.
- DeNiro M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495–506.
- DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45: 341–351.
- Durell, S. E. L. V. D. 2000. Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biological Reviews of the Cambridge Philosophical Society* 75: 503–518.
- Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management* 53: 962–968.
- Estes, J. A., M. L. Riedman, M. M. Staedler, M. Tinker, and B. E. Lyon. 2003.

- Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology* 72: 144–155.
- Farley, S. D., and Robbins, C. T. 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Canadian Journal of Zoology* 73: 2216–2222.
- Felicetti, L. A., C. C. Schwartz, R. O. Rye, M. A. Haroldson, K. A. Gunther, D. L. Phillips, and C. T. Robbins. 2003. Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. *Canadian Journal of Zoology* 81: 763–770.
- Fortin, J. K., S. D. Farley, K. D. Rode, and C. T. Robbins. 2007. Dietary and spatial overlap between sympatric ursids relative to salmon use. *Ursus* 18: 19–29.
- Fry, B. 2006. *Stable isotope ecology*. Springer, New York, New York, USA. 308pp.
- Gau, R. J., R. Case, D. F. Penner, and P. D. McLoughlin. 2002. Feeding patterns of barren-ground grizzly bears in the central Canadian Arctic. *Arctic* 55: 339–344.
- Golley, F. B. 1961. Energy values of ecological materials. *Ecology* 42: 581–584.
- Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* 74: 2080–2088.
- Hilderbrand, G. V., S. G. Jenkins, C.C. Schwartz, T. A. Hanley, and C. T. Robbins.

- 1999b. Effect of seasonal differences in dietary meat intake on change in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology* 77: 1623–1630.
- Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999a. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77: 132–138.
- Hobson, K. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*. 120: 314–326.
- Hobson, K. A., B. N. McLellan, and J. G. Woods. 2000. Using stable isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology* 78: 1332–1339.
- Hobson, K. A., J. F. Piatt, and J. Pitocchelli. 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63: 786–798.
- Hobson, K., and L. I. Wassenaar. 1999. Stable isotope ecology: an introduction. *Oecologia* 120: 312–313.
- Holcroft, A. C., and S. Herrero. 1991. Black bear, *Ursus americanus*, food habits in southwestern Alberta. *Canadian Field-Naturalist* 105: 335–345.
- Jacoby, M. E., G. V. Hilderbrand, C. Servheen, C. C. Schwartz, S. M. Arthur, T. A. Hanley, C. T. Robbins, and R. Michener. 1999. Trophic relations of

- brown and black bears in several western North American ecosystems. *Canadian Journal of Zoology* 63: 921–929.
- Jenkins, S.G., S. T. Partridge, T. R. Stephenson, S. D. Farley, and C. T. Robbins. 2001. Nitrogen and carbon stable isotope fractionation between mothers and neonates. *Oecologia* 129: 336–341.
- Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78: 1–27.
- Lariviere, S. 2001. *Ursus americanus*. *Mammalian Species* 647: 1–11.
- Lomnicki, A. 1988. Population ecology of individuals. Princeton University Press. Princeton, New Jersey, USA.
- Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biological Conservation* 81: 161–177.
- Mattson, D. J., C. M. Gillin, S. A. Benson, and R. R. Knight. 1991. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology* 69: 2430–2435.
- Mattson, D. J., and D. P. Reinhart. 1995. Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975 – 1989. *Canadian Journal of Zoology* 73: 2072–2079.
- Mattson, D. J., and D. P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Applied Ecology* 34: 926–940.
- Mazur, R., and V. Seher. 2008. Socially learned foraging behaviour in wild black bears, *Ursus americanus*. *Animal Behaviour* 75: 1503–1508.

- McLellan, B. N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. II. Mortality rates and causes of death. *Canadian Journal of Zoology* 67: 1861–1864.
- Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. *Geochimica et Cosmochimica Acta* 48: 1135–1140.
- Mowat, G., and D. C. Heard. 2006. Major components of grizzly bear diet across North America. *Canadian Journal of Zoology* 84: 473–489.
- Mowat, G. and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. *Journal of Wildlife Management* 64: 183–193.
- Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy* 87: 1112–1121.
- Natural Regions Committee 2006. Natural Regions and Subregions of Alberta. Compiled by D. J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. T/852.
- Neufeld, L. M. 2006. Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta. M.Sc. Thesis. University of Alberta. Edmonton Alberta.
- Nielsen, S. E. 2005. Habitat ecology, conservation, and projected population viability of grizzly bear (*Ursus arctos*) in west-central Alberta, Canada. Dissertation. University of Alberta. Edmonton, Alberta.

- 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.
- Ostrum, P. H., M. Colunga-Garcia, and S. H. Gage. 1997. Establishing pathways of energy flow for insect predators using stable isotope ratios: field and laboratory evidence. *Oecologia* 109: 108–113.
- Parker, G. R. 1981. Physical and reproductive characteristics of an expanding woodland caribou (*Rangifer tarandus caribou*) population in northern Labrador. *Canadian Journal of Zoology* 59: 1929–1940.
- Pasitschniak-Arts, M. 1993. *Ursus arctos*. *Mammalian Species* 439: 1–10.
- Pelton, M. R. 2000. Black bear. Ecology and management of large mammals in North America (eds S. Dumarais and P.R. Krausman). Prentice-Hall Inc. Upper Saddle River, New Jersey, USA. 778pp.
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293–320.
- Phillips, D. L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* 127: 166–170.
- Phillips, D. L., and J.W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136: 261–269.
- Phillips, D. L., S. D. Newsome, and J. W. Gregg. 2005. Combining sources in stable isotopes mixing models: alternative methods. *Oecologia* 144: 520–527.

- Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology* 68: 1645–1651.
- Rau, G. 1978. Carbon-13 depletion in a subalpine lake: carbon flow implications. *Science* 201: 901–902.
- Robbins, C. T. 1983. *Wildlife feeding and nutrition*. Academic Press, Orlando, Florida, USA.
- Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus* 15: 161–171.
- Rode, K. D., C. T. Robbins, and L. A. Shipley. 2001. Constraints on herbivory by grizzly bears. *Oecologia* 128: 62–71.
- Rosing, M. M., M. Ben-David, and R. P. Barry. 1998. Analysis of stable isotope data: a K nearest-neighbours randomization test. *Journal of Wildlife Management* 62: 380–388.
- Smith, K. G., E. J. Ficht, D. Hobson, T. C. Sorensen, and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. *Canadian Journal of Zoology* 78: 1433–1440.
- Stotyn, S. 2008. Ecological interactions of mountain caribou, wolves and moose in the North Columbia Mountains, British Columbia. M.Sc. Thesis, University of Alberta, Edmonton, Alberta.
- Thompson, D. R., S. J. Bury, K. A. Hobson, L. I. Wassenaar, and J. P. Shannon. 2005. Stable isotope in ecological studies. *Oecologia* 144: 517–519.
- Tiezan, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade. 1983. Fractionation

- and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57: 32–37.
- Urton, E. J. M., and K. A. Hobson. 2005. Intrapopulation variation in gray wolf isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) profiles: implications for the ecology of individuals. *Oecologia* 145: 317–326.
- Vander Zanden, M. J., and Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83: 2152–2161.
- Welch, C. A., J. Keay, K. C. Kendall, and T. C. Robbins. 1997. Constraints of frugivory on bears. *Ecology* 78: 1105–1119.
- White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288–331 in *Research techniques in animal ecology: controversies and consequences* (eds L. Boitani and T. K. Fuller). Columbia University Press. New York, New York, USA.
- White, D. Jr., K. C. Kendall, and H. D. Picton. 1998. Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. *Canadian Journal of Zoology* 76: 221–227.
- White, D. Jr., K. C. Kendall, and H. D. Picton. 1999. Potential energetic effects of mountain climbers on foraging grizzly bears. *Wildlife Society Bulletin* 27: 146–151.
- Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. *Wildlife Society Bulletin* 27: 616–627.
- Young, B. F., and R. L. Ruff. 1982. Population dynamics and movements of black

bears in east central Alberta. *Journal of Wildlife Management* 46:
845–860.

CHAPTER 3: SPATIAL AND TEMPORAL PATTERNS OF WOLF HARVEST ON REGISTERED TRAPLINES IN ALBERTA, CANADA

INTRODUCTION

Wolf management has become the subject of much attention as gray wolf (*Canis lupus*) populations have expanded across numerous US states and in many parts of Europe (Boitani 2003). Increases in wolf numbers and expansions of wolf ranges generally come with increased human-wolf conflicts (Mech 1995, Harper et al. 2005); however, addressing these conflicts is often socially and politically difficult due to the intense polarization of societal values and beliefs surrounding wolves (Blanco et al. 1992, Cozza et al. 1996, Fritts et al. 2003, Treves and Koaranth 2003, Bisi et al. 2007). Growing wolf populations and divided opinions surrounding wolves highlight the need for sound management frameworks that address both the future persistence of the species and the resolution of human-wolf conflicts. In this chapter I discuss Alberta's approach to wolf management and summarize spatial and temporal patterns of wolf harvest on registered traplines.

In Alberta, Canada, the wolf is classified as game species and a provincial management plan has been in place since 1991 (Gunson 1991). Provincial populations have been managed mainly through trapping and to a lesser extent hunting. According to the provincial management plan 25–35% of the wolf population can be harvested annually to ensure a sustainable harvest without depleting the population. Because harvests are substantially below this level,

hunting and trapping regulations contain no bag limits or quotas for the species. Wolf control (deliberately removing most of a subpopulation) requires unusual or serious circumstances, such as the recovery of a threatened or endangered prey species or disease management, and must go through a full public review (Gunson 1991). Wolves can be shot on private land without a permit to protect private property such as livestock or pets and Alberta Fish and Wildlife officers may aid in trapping and killing wolves in areas of chronic livestock depredation. A livestock compensation program is supported by the Alberta Conservation Association to reimburse livestock losses due to wolf predation (<http://www.ab-conservation.com/go/default/index.cfm/programs/report-a-poacher-and-compensation-programs>).

Furbearer harvest on Crown land in Alberta and in most other Canadian provinces is managed through a system of registered traplines. The system was established in 1939 to eliminate competition for wild fur harvest by giving exclusive trapping rights over a delimited area known as a registered fur management area (RFMA) or registered trapline (Poole and Mowat 2001). Today, Alberta has approximately 1,700 traplines across 8 fur management zones (Figure 3–1) that are defined as “large tracts of land having similar environmental features” (Alberta Sustainable Resource Development 2007). Furbearer harvest is managed through quotas and seasons within wildlife management units (WMUs) for each zone. The average size of an RFMA is 223 km² but they range from 3 km² to 4,145 km². A senior license holder, also known as senior trapper, is the

principal holder of an RFMA and can form partnerships with other individuals (junior trappers) who then can hold a trapping license for the same area.

The idea of examining wolf trapping records in Alberta stemmed from the implementation of a local wolf-control program in winter 2005-2006. A known 362 wolves have been removed from a 5,000 km² area in west-central Alberta over the last 4 winters, mainly using aerial gunning and strychnine poisoning (D. Hervieux, Alberta Sustainable Resource Development, unpublished data). The justification for this ongoing management plan is to conserve a threatened woodland caribou (*Rangifer tarandus caribou*) herd; however, the long-term effectiveness of such predator control programs is questionable because wolf numbers rebound quickly after culling ends (National Research Council 1997). In addition, wolf control programs are costly (National Research Council 1997, Dekker 2007, Mosnier et al. 2008) and generally foster negative responses from the public (National Research Council 1997, Martínez-Españeira 2006, Van Ballenberghe 2006).

In light of recent provincial wolf management decisions and wolf management issues worldwide it seems timely to examine Alberta's wolf-harvest records to better understand spatial and temporal trends in wolf trapping. The goal of this exercise is to understand better the dynamics of wolf trapping in Alberta and to evaluate the role of trapping in wolf management. I analyzed wolf harvests from registered traplines between 1985 and 2006. I use 1985 as a starting point because prior to this, wolf populations had been severely reduced as part of rabies control measures, and predator control to increase ungulate

populations continued well into the 1960s (Gunson 1992). Not until the mid 1980s had wolves returned to most forested portions of Alberta, such as Banff National Park (Duke et al. 2001), and presumably their distribution was beginning to occupy most registered traplines by that time.

Wildlife harvests show particular spatial patterns and the tendency is that harvest density is highest near human settlements due to higher hunter effort (Brøseth and Pedersen 2000, Sirén et al. 2004, Golden et al. 2007, Smith et al. 2008). It has been suggested that source-sink dynamics operate in many harvested systems because more remote areas, with little harvest pressure, produce an abundance of animals that disperse to areas with higher hunting intensity (Begazo and Bodmer 1998, Novaro et al. 2000). Spatial structure has been introduced in recent harvest models (Siren et al. 2004, Kellner et al. 2007, Costello and Polasky 2008, Ling and Milner-Gulland 2008) to account for (1) uneven distribution of hunting effort, which tends to create density gradients in animals, and (2) animal dispersal, which tends to smooth these gradients (Sirén et al. 2004). I expected non-random patterns of wolf harvest on the landscape as a result of interactions between trapping pressure and wolf density. Because trapping has become largely recreational I expected trapping to be concentrated in areas of high trapper density near human population centers.

STUDY AREA

The study was conducted on registered fur management areas in Alberta, Canada (Figure 3–1). Registered traplines span most of the province and include a wide

variety of cover types including northern boreal forest, mountains, foothills, and a small portion of prairie and parkland vegetation types. Alberta is divided into 2 land-use zones: the white zone and the green zone. The green zone comprises approximately 60% of the province and is managed for timber production, watersheds, wildlife and fisheries, recreation, and limited agricultural grazing. The white zone is the settled portion of the province where both public and private lands are managed mostly for agriculture. Wolves are primarily limited to the green zone with few subpopulations occurring in the white zone. Registered traplines mostly are distributed within the green zone. Presumably, wolves have been largely excluded from the white zone due to the presence of densely populated human centers and inadequate habitat. Even in areas that potentially could support wolves, e.g., where the land has not been cleared, human-wolf conflicts appear to have precluded the establishment of permanent wolf subpopulations in the white zone.

METHODS

We obtained wolf harvest records (1985 to 2006) from registered traplines across Alberta from Alberta Sustainable Resource Development. I used descriptive statistics and maps created in a geographic information system (GIS) to examine and summarize the data spatially and temporally at 3 scales: provincial, regional (by WMU), and local (by RFMA). All statistical analyses were conducted using STATA SE 10.0 (StataCorp, College Station, Texas).

Provincial Harvest Summary

We examined the change in several wolf harvest metrics (total harvest, number of traplines with harvest, and average number of wolves taken per trapline) over time. I used regression methods to describe trends in time series of these metrics.

Pelt price data (1970-2006) were obtained from Statistics Canada's (2008) census of wildlife pelt production. Prices were adjusted to represent 2006 dollar equivalents based on inflation rates reported by the Bank of Canada (http://www.bankofcanada.ca/en/rates/inflation_calc.html). I used cross-correlation analysis to investigate the relationship between detrended time series of wolf harvest and pelt price. I compared annual wolf harvest in Alberta and annual change in harvest to current and previous year's pelt prices. I also compared wolf harvests and changes in wolf harvests to current and previous year's pelt prices for marten (*Martes americana*) and lynx (*Lynx canadensis*) because these are valuable furbearer species that might affect trapper effort.

Provincial harvest rates by registered trappers (2002-2006) were estimated based on a wolf population estimate extrapolated from two recent wolf studies (Webb 2008; Latham 2008). Average wolf territory size in the east slopes (foothills of west-central Alberta) was 640 km² (range: 350-1,500 km²; Webb 2008). In northeastern Alberta average territory size was 739 km² (range: 263-1,071 km²; Latham 2008). Average winter pack sizes for both areas are similar with 7.9 wolves and 7.8 wolves for the east slopes and northeastern Alberta respectively (Webb 2008, Latham 2008). I averaged territory size (689.5 km²) and pack size (7.85 wolves) to estimate the population on the entire provincial wolf range. I assumed wolves to cover approximately 60% (399,000 km²) of

Alberta's landmass (Gunson 1991) and adjusted by +13% for lone wolves (Fuller and Keith 1980, Fuller et al. 2003). Wolf harvest rates from 1985 to 1993 were estimated based on an earlier wolf population estimate of 4,200 individuals (Gunson 1991).

Harvest by Wildlife Management Unit

In a GIS, I created annual harvest density (harvest per area) maps from 1985 to 2006 to better understand temporal patterns of wolf trapping. I defined 6 harvest-density classes to classify wolf harvest density: very high (>4.5 wolves/1000 km²), high (>3.0 – 4.5 wolves/1000 km²), medium (>1.5 – 3.0 wolves/1000 km²), low (>0.5 – 1.5 wolves/1000 km²), very low (>0 – 0.5 wolves/1000 km²), and none (0 wolves/1000 km²). I summarized total harvest density for 2 time periods 1985–1995 and 1996–2006 to demonstrate how wolf harvest distribution has changed on the landscape.

Harvest by Registered Trapline

We analyzed wolf harvests at the RFMA level using spatial autocorrelation to determine if trapline harvests are spatially correlated. Wolf territory size in Alberta averages between 640 and 739 km² (Webb 2008, Latham 2008) compared with average RFMA size of 223 km² (± 5.7 km², *SE*). I expected autocorrelation among trapline harvests to decline at distances greater than the average wolf territory size because of variation in wolf density (i.e., trappers are targeting different packs). Assuming that wolf territory shapes are approximately circular, the average territory sizes from the Latham (2008) and Webb (2008) studies would translate into diameters (or distances) of 28.5 to 30.7 km.

We calculated Moran's I autocorrelation coefficients using Passage 2 (Beta version 2.0.7.28; <http://www.passagesoftware.net>). First I assigned annual harvests to each trapline and identified the centroid point of each trapline polygon in a GIS and calculated the Euclidian distance between each pair of centroids. I used these distance measurements as the distance between traplines to create a distance matrix based on 29 distance classes at 5 km intervals between 10 km and 150 km. For each year of data (1985-2006) Moran's I was calculated at every distance class. I present results as a summarized output of average ($n = 22$ years) Moran's I coefficients for each distance class.

I examined the temporal dynamics of trapping on individual traplines with an autocorrelation function (STATA SE 10.0) using a subset of traplines ($n = 79$) that had consistent harvest (≥ 1 wolf harvested/year in ≥ 10 years) between 1985 and 2006. I calculated the autocorrelation in the annual change in harvest over 8 annual time lags. I hypothesized that the first lag would show a significant negative autocorrelation value because harvest success in one year reduces potential harvest in the consecutive year because of the reduction in wolf abundance and possibly behavioral avoidance by wolves (Adams et al. 2008).

RESULTS

Provincial Harvest Summary

During 1985 to 2006 10,140 wolves were trapped on 1,046 registered traplines in Alberta ($\bar{x} = 9.7$ wolves/trapper ± 1.0 , 95% CI); however, most of these traplines did not have consistent harvests over time. Trappers averaged a harvest every 3.7

years (± 0.2 , 95% CI) during the period of study. Most RFMAs in Alberta did not have any wolf harvest ($n = 597$) or else had only 1 or 2 years when trappers caught wolves ($n = 527$). Wolves were trapped in at least half of the 22 years in only 61 RFMAs.

Alberta's annual wolf harvest varied from year to year but the overall trend showed an increase in harvest over time ($\beta = 21.05$, $r = 0.79$, $n = 22$) with a minimum of 195 wolves trapped in 1991 and a peak harvest of 803 wolves in 2006 (Figure 3-2). The number of traplines with wolf harvest also fluctuated annually and the general pattern followed that of the annual wolf harvest (Figure 3-2; $\beta = 3.81$, $r = 0.65$, $n = 22$). I also observed an increase in the average number of wolves trapped per trapline ($\beta = 0.06$, $r = 0.82$, $n = 22$). In any given year traplines with wolf harvest only made up a small proportion of the total traplines, ranging from 6–14% of provincial RFMAs. I found no correlation between wolf harvest and current pelt price ($r_{20} = -0.381$, $P = -0.381$) or previous year's pelt price ($r_{20} = -0.395$, $P = 0.069$). Similarly, I found no correlation between change in harvest and current pelt price ($r_{19} = 0.071$, $P = 0.761$) or previous year's pelt price ($r_{19} = -0.186$, $P = 0.421$). Likewise, no relationships were found between marten or lynx fur prices and wolf harvests over the 22 years of data.

Based on recent estimates of wolf home ranges in Alberta (Latham 2008; Webb 2008), I estimated a population of approximately 5,133 wolves in the province. This number represents a winter population estimate, and I would expect the population to reach higher numbers in late spring and summer after

pups are born. Based on my winter population estimate, harvest rates on registered traplines between 2002 and 2006 have ranged from 11.3% to 15.6% of the provincial population. Between 1985 and 1992 harvest rates on RFMAs ranged from 4.6% to 10.9% of the provincial wolf population. The average harvest rate ($n = 13$ years) was 9.8% of the provincial population.

Harvest by Wildlife Management Unit

We studied the spatial distribution of harvests by examining harvest density at the WMU level ($n = 190$). Over time I observed a clear increase in wolf harvest across most of the landscape (Appendix F) and a marked increase in the number of very high harvest events (> 45 wolves/1000 km²; Figure 3-3). Average harvest density in 1985 was only 0.39 and reached a maximum of 1.39 wolves/1000 km² in 2005 ($\beta = 0.04$, $r = 0.77$, $n = 22$). Although the number of WMUs with high and very high harvest increased with time, their spatial distribution remained relatively unchanged (Figure 3-3). Harvests were consistently concentrated in the mountains and along the foothills boundary, in addition to a few in the boreal region of east-central Alberta forming a crescent-shaped belt around the cities of Edmonton and Calgary.

Harvest by Registered Trapline

The finest-scale spatial pattern I analyzed was at the RFMA level with the use of a spatial autocorrelation analysis. Average Moran's I values peaked at the 20-25 km distance class, about 3 times the size of the average RFMA and slightly less than the average distance between centroids for a pack size of 640km² (Figure 3-4). Although correlation values are low reflecting high spatial and temporal

variability, the autocorrelation pattern is clearly structured and significantly different than zero as indicated by the 95% confidence interval.

As expected, my analysis of temporal patterns of wolf harvest on individual traplines indicates that the change in wolf harvest in consecutive years is negatively autocorrelated (Figure 3–5). The 95% confidence intervals for all other time lags overlap with zero indicating no autocorrelation and no evidence of periodicity. The autocorrelation pattern observed suggests that if harvest increased one year it is likely to decrease the following year or vice versa.

DISCUSSION

Wolf harvest on registered traplines has increased considerably in Alberta over the past 22 years. The number of traplines with wolf harvest has increased, and the number of wolves taken per trapline also has increased. To my knowledge trapper effort has not increased over the past two decades, in fact, effort appears to have decreased by 10% from 1980 to 2000 (Poole and Mowat 2001). Thus observed harvest trends suggest an increasing provincial wolf population. Wolf population expansion could be linked to increased ungulate populations, particularly deer (*Odocoileus* spp.). Wolf territory size tends to decrease with increasing prey density (Walters et al. 1981). Significant increases in deer density were observed in northeastern Alberta since the early 1990s but no change in moose density (Latham 2008). Similarly, repeated aerial survey data collected since 1969 (Charest 2005) suggest an increase in white-tailed deer (*O. virginianus*) abundance. Increases in wolf numbers also are thought to be

inherently linked to changes in provincial wolf management strategies that have occurred over the past 5 decades. Wolf bounties ended in 1954, large-scale poisoning for rabies control occurred 1952-1956, and wolf control to enhance big game populations ended in 1966 (Gunson 1991). Wolf management then shifted towards wolf protection (Gunson 1992) with the current wolf management plan established in 1991. Although exceptions apply for endangered species protection and chronic livestock depredation, the management plan largely protects the species against intensive human control measures and as such, wolves have had the chance to increase during the last 17 years to a level near ecological carrying capacity (Caugley 1979). Social interactions among wolves are believed to dictate carrying capacity (Packard and Mech 1983) and a number of observations support that idea that wolves have saturated Alberta's landscape. Latham (2008) and Webb (2008) demonstrate that wolf territories are tightly packed together offering few openings for further pack establishment. Further, an ongoing wolf-control program over 5,000 km² of west-central Alberta has sustained the removal of 60-120 wolves annually during the last 4 years, with rapid recolonization demonstrating the presence of robust subpopulations on the surrounding landscape (Robichaud and Boyce 2009). The combination of an increasing prey base and a more conservation-focused management plan for wolves have contributed to the species' population increase.

Alberta's wolf population has been harvested at an average annual rate of 9.8% by registered trappers (range: 4.6% to 15.5%). Sustainable harvest rates for wolves vary greatly across populations. Fuller et al. (2003) reviewed the effects

of harvest on wolf populations and reported sustainable harvest values ranging from 16-74% across various areas in northern North America, with most values being over 30%. Harvest rates observed in Alberta are well below the level that would cause population decline and demonstrate that registered trappers do not have a sufficient impact to deplete wolf numbers. The registered trapline system ensures the dispersion of harvest across the landscape thereby preventing local extirpation in some areas and underutilization in others. From a conservation standpoint the registered trapline system in Alberta is an effective management tool that does not threaten the persistence of wolves. In extreme cases, a few trappers might harvest large numbers of wolves but this harvest pressure is exercised on such a small portion of the landscape that wolves from surrounding RFMAs rapidly recolonize the area owing their high dispersal rates (Gese and Mech 1991, Boyd and Pletscher 1999, Adams et al. 2008).

On the other hand, if managers are interested in substantially reducing certain wolf subpopulations, then the Alberta trapline system is not the answer. Trappers in much of Alberta do not have a large enough impact to reduce regional (WMU) wolf abundance, let alone decrease provincial wolf numbers. In addition, it is difficult to maintain consistent wolf harvests over time on individual traplines because high harvest years tend to be followed by a decrease in trapping success. To effectively reduce wolf numbers, trapper effort would need to increase considerably and Alberta's trapline system is not designed to target increased trapping pressure in problem areas. The Alberta system contrasts with the one found in Alaska, where trappers can harvest anywhere so long as they follow

area-specific regulations and seasons (Alaska Department of Fish and Game 2008).

We found that wolf harvest densities were highest in the Rocky Mountains and adjacent foothills area. This might reflect wolf distribution on the landscape, but other factors also could be driving this pattern. Active wolf harvest regions are found in wilderness areas within 400km of the Edmonton and Calgary human population centers, whereas most of northern Alberta has low human density. Traplines in areas of high harvest density tend to be smaller than in northern Alberta, indicating that the harvest pattern might be due to higher densities of trappers on the landscape. These observations are consistent with my prediction that wolf harvest distribution should reflect trapping pressure and wolf density. High harvests were observed in areas with high trapper participation and are presumably maintained by wolf dispersal and infilling (National Research Council 1997, Hayes et al. 2003). Although wolf harvest is not uniformly distributed across the province, the current pattern may play an important role in reducing human-wolf conflicts, particularly in Alberta's white zone. By removing wolves near human population centers, trappers remove potential dispersers and influence the distribution of wolves in densely settled portion of the province.

There was no obvious change in northern trapping, which could be linked to lower numbers of Métis and First Nations trappers (Poole and Mowat 2001). Since the mid 1990s the number of First Nations and Métis trapping licenses has been declining steadily, with a 75% difference between 1994-1995 and 2006-

2007 (Alberta Sustainable Resource Development 2002-2007, Alberta Environment 1999-2000, Alberta Department of Environmental Protection 1996-1998). Differences in landscape features such as access and industrial development can play an important role in determining harvest success. For examples, marten harvest in west-central Alberta was higher on traplines with more mature-conifer forest cover, less fragmentation, and fewer oil/gas well sites (Webb and Boyce 2009). Similarly, reduced trapper effort was linked to higher levels of industrial development (Webb et al. 2008).

Wolf harvests discussed in this paper are from registered traplines only and do not include wolves harvested by hunters or wolves shot or trapped on private land because there is no requirement that these harvests are reported. Wolf harvest in southern Alberta is therefore underrepresented in this analysis because most of the area consists of private land where landowners can shoot wolves to protect livestock and pets. Most wolves are harvested on registered traplines because the agricultural areas of Alberta do not support large wolf populations and harvest by recreational hunters is low in heavily forested areas (Gunson 1992). Estimates of wolves harvested by hunters in the mid to late 1980s were approximately 100 wolves per year (Gunson 1992).

Similar to Gunson (1992) and Poole and Mowat (2001), I found no link between pelt prices and wolf harvest. Although harvest has increased, from a fur production standpoint wolves have been an underutilized resource (Gunson 1992). Even with a conservative population estimate of 5,000-6,000 wolves in Alberta, trappers could sustainably take 1,000 to 1,250 animals annually at conservative

harvest rates of 20–25% as outlined in the provincial wolf management plan (Gunson 1991), and the potential yields may be twice this (Fuller et al. 2003). Despite there being no bag limits on wolves, trapper harvests are well below sustainable harvest rates. Several reasons have been suggested to explain low wolf harvests including wariness and difficulty of capture, irregular occurrence of wolves within certain trapping areas, and the high mobility of the species (Gunson 1992). I believe that the inability to concentrate trapping efforts in high wolf density areas (due to the registered traplines system) is a contributing factor to low overall wolf harvests, in addition to the fact that many trappers are not targeting the species.

Wolf harvest on registered traplines presented complex spatial and temporal patterns, which can be partially explained by wolf biology. The spatial pattern is partly structured by wolf territory size. Peak autocorrelation of harvests on traplines fell within the 20–25 km distance class, just below the average distance between wolf home ranges of 25–30 km as reported by Latham (2008) and Webb (2008). Spatial distribution of harvests is limited by pack size within a home range whereas lower autocorrelation values associated with distances < 20 km between traplines could be explained by a “trapper effect”. On RFMAs that are <20 km from other each other, multiple trappers could potentially harvest wolves from the same pack. The high success of one trapper would then contribute to lower success of adjacent trappers. At distances past the average territory size trappers are presumably harvesting different packs thus variation in wolf density

and differences in landscape features become drivers of wolf harvest success and contribute to lower autocorrelation values between traplines.

The temporal pattern of harvest is associated with a strong negative autocorrelation in annual change in harvest at the 1 year lag. In a successful year trappers harvest several wolves, which contributes to their decreased success the following year while the local wolf population recovers from the harvest. In addition, remaining wolves might become more wary if they had non-lethal experience with trapping (Adams et al. 2008).

Management Implications

Our study emphasizes the usefulness of the registered trapline system facilitating management for wolves. The registered trapline system has arguably reduced the variability in the population consequences of harvest by distributing the trapper harvest over a large number of individual RFMAs throughout the range of the species. As a consequence, trapping has not had a negative impact on the distribution or abundance of wolves in Alberta.

The pattern of highest harvest around the intersection of wolf and non-wolf habitat might contribute to reducing conflicts with humans and agriculture.

Trapper harvest did not appear to have appreciable negative effects on the overall Alberta wolf population despite there being no quotas or bag limits for the species. The registered trapline system ensures relatively even dispersion of harvest across the landscape which I believe has had conservation benefits. Training trappers how to trap wolves might increase their effectiveness at removing wolves at a local scale. But when control actions are deemed necessary

trappers are unlikely to remove a sufficient number of wolves over a large enough area to limit subpopulations under the registered trapline system.

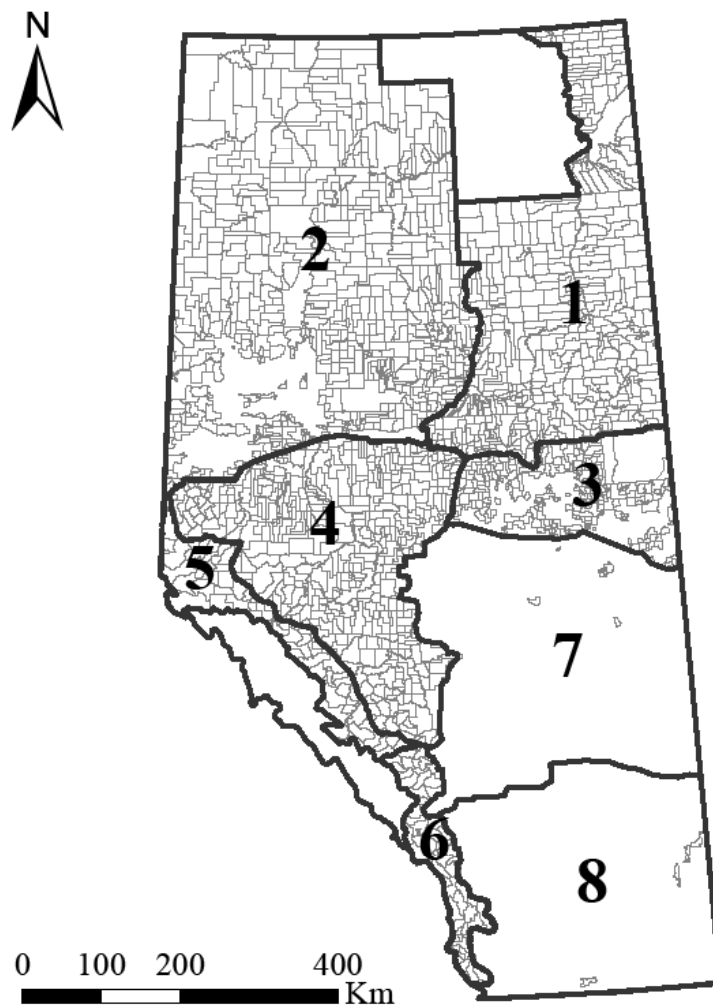


Figure 3–1. Map of Alberta showing all Registered Fur Management Areas (small gray divisions) divided in eight provincial Fur Management Zones (labeled 1-8). Unlabelled white areas are National Parks.

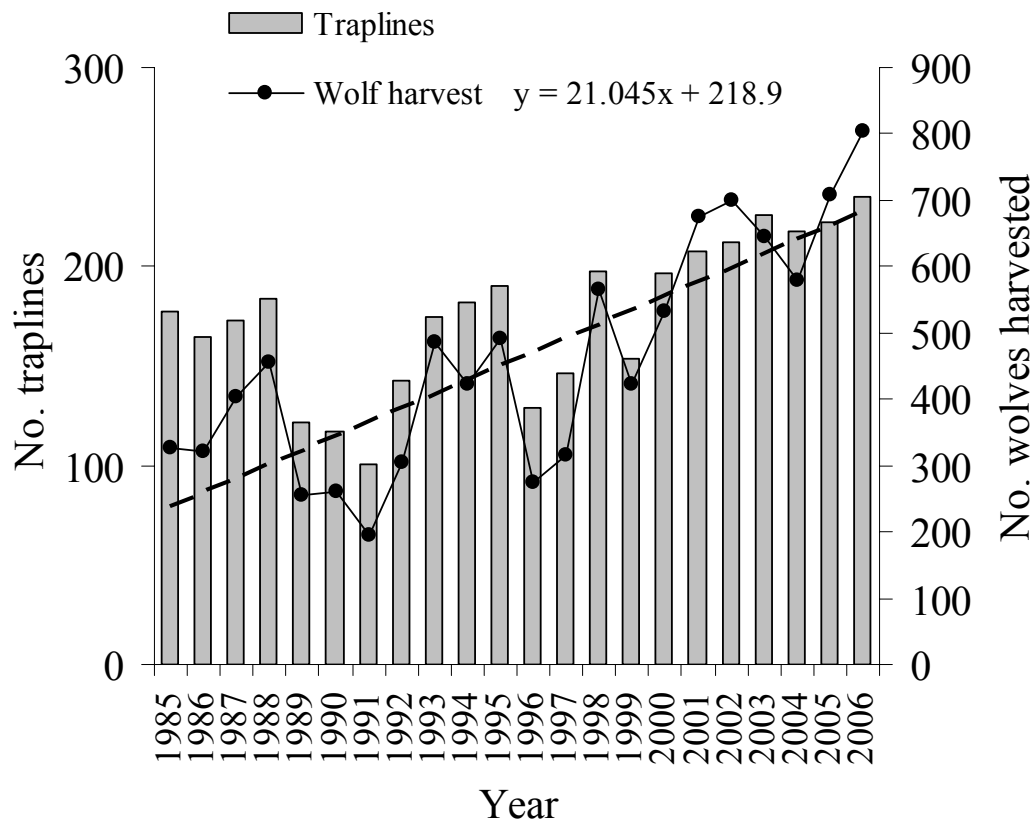


Figure 3–2. Annual wolf harvest (closed circles and right y-axis) and total number of traplines reporting harvest in Alberta (bar graph and left y-axis) from 1985 to 2006.

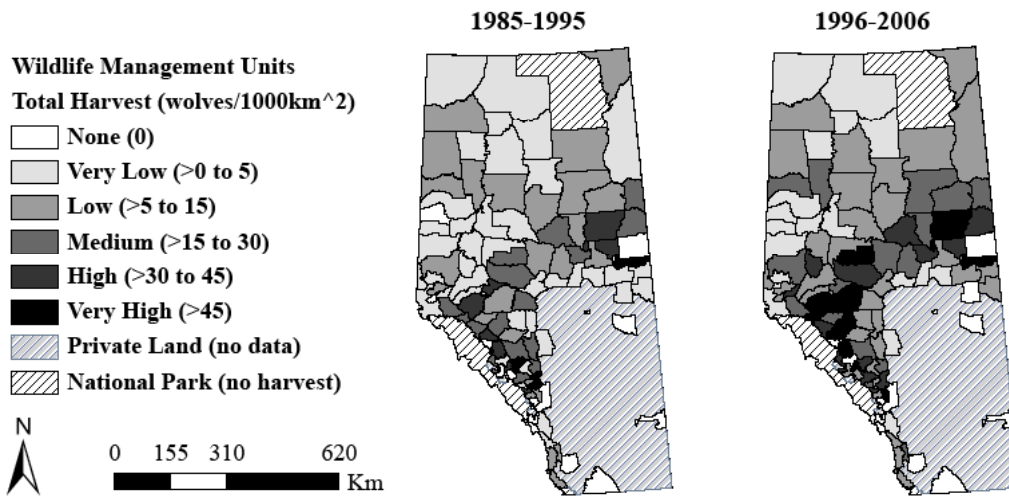


Figure 3–3. Comparison of total wolf harvest density from Alberta’s wildlife management units in 1985-1995 and 1996-2006.

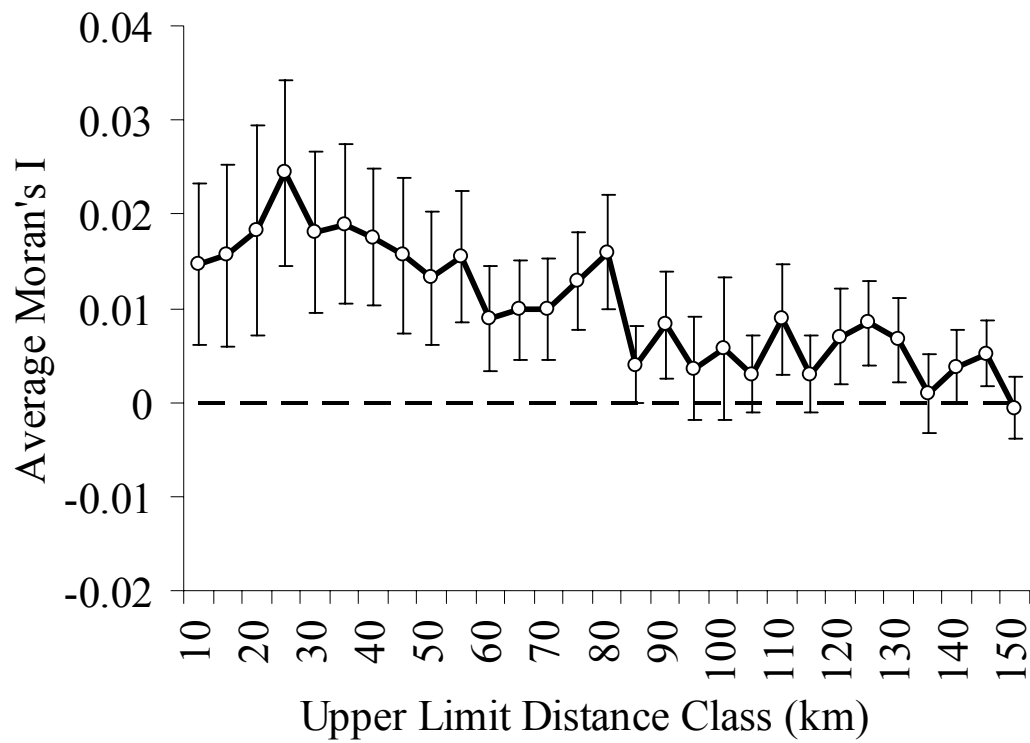


Figure 3–4. Average Moran's I correlation values ($n = 22$ yrs) identifying the autocorrelation between wolf harvests on registered traplines and lagged distance between traplines. The error bars indicate the 95% confidence interval around each average value.

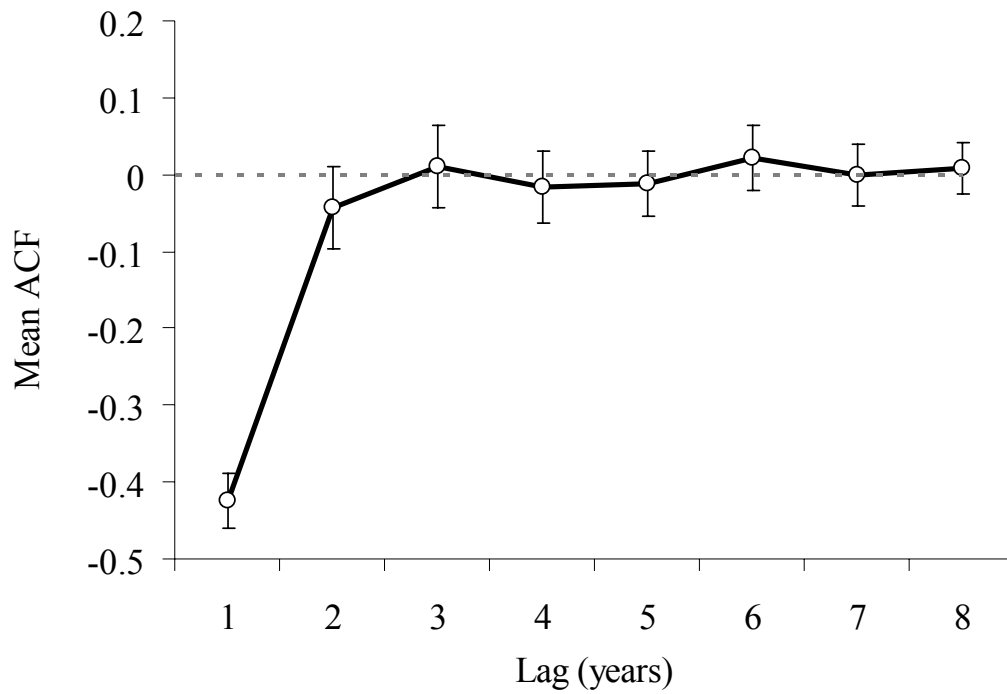


Figure 3–5. Average autocorrelation values ($n = 79$ traplines) from an autocorrelation function (ACF) indicating the relationship between annual change in wolf harvest and number of years between harvests. The error bars indicate the 95% confidence interval around each average value.

LITERATURE CITED

- Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in central Brooks Range, Alaska. *Wildlife Monographs* 170: 1–25.
- Alaska Department of Fish and Game. 2008. 2008-2009 Alaska trapping regulations. Publication No. 49. Juneau, Alaska, USA.
- Alberta Department of Environmental Protection. 1996-1998. Alberta guide to 1996-1998 trapping regulations. Fish and Wildlife Division, Edmonton, Alberta, Canada.
- Alberta Environment. 1999-2000. Alberta guide to 1999-2001 trapping regulations. Fish and Wildlife Division, Edmonton, Alberta, Canada. (annual regulations).
- Alberta Sustainable Resource Development. 2002-2007. Alberta guide to 2002-2008 trapping regulations. Fish and Wildlife Division, Edmonton, Alberta, Canada.
- Begazo, A. F., and R. E. Bodmer. 1998. Use and conservation of cracidae (aves: galliformes) in the Peruvian amazon. *Oryx* 32: 301–309.
- Bisi, J., S. Kirki, M. Svensburg, and T. Liukkonen. 2007. Human dimensions of wolf (*Canis lupus*) conflicts in Finland. *European Journal of Wildlife Research* 53: 304–314.
- Blanco, J. C., S. Reig, and L. de la Cuesta. 1992. Distribution, status, and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation* 60: 73–80.

- Boitani, L. 2003. Wolf conservation and recovery. Pages 317–340 *in* L. D. Mech and L. Boitani editors. *Wolves: behaviour, ecology and conservation*. University of Chicago Press, Chicago, Illinois, USA.
- Boyd, D. K., and D. H. Pletscher. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. *Journal of Wildlife Management* 63: 1094–1108.
- Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors. *Biological Conservation* 83: 279–289.
- Brøseth, H., and H. C. Pedersen. 2000. Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS. *Journal of Applied Ecology* 37: 182–190.
- Charest, K. S. 2005. Changes in moose and white-tailed deer abundance in northeastern Alberta and the relationship to cumulative impacts. Thesis, University of Alberta, Edmonton, Canada.
- Costello, C., and S. Polasky. 2008. Optimal harvesting of stochastic spatial resources. *Journal of Environmental Economics and Management* 56: 1–18.
- Cozza, K., S. Fico, M.-L. Battistini, and E. Rogers. 1996. The damage-conservation interface illustrated by predation on domestic livestock in central Italy. *Biological Conservation* 78: 329–336.
- Dekker, D. 2007. An historical perspective on Alberta's current wolf wars. *Nature Alberta* 36: 12–13.
- Duke, D. L., M. Hebblewhite, P. C. Paquet, C. Callaghan, and M. Percy. 2001.

- Restoration of a large-carnivore corridor in Banff National Park. Pages 261–275 in D. S. Maehr, R. F. Noss, and J. F. Larkin editors. Large mammal restoration: Ecological and sociological challenges in the 21st century. Island Press, Washington, D.C., USA.
- Fritts, S. H., R. O. Stephenson, R. D. Hayes, and L. Boitani. 2003. Wolves and humans. Pages 289–316 in L. D. Mech and L. Boitani editors. Wolves: behaviour, ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.
- Fuller, T.K., and L.B. Keith. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *Journal of Wildlife Management* 44: 583–602.
- Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–190 in L. D. Mech and L. Biotani, editors. Wolves: behaviour, ecology and conservation, University of Chicago Press, Chicago, Illinois. USA.
- Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. *Canadian Journal of Zoology* 69: 2946–2955.
- Golden, H. N., A. M. Christ, and E. K. Solomon. 2007. Spatiotemporal analysis of wolverine *Gulo gulo* harvest in Alaska. *Wildlife Biology* 13 (Sp 2): 68–75.

- Gunson, J. R. 1991. Management plan for wolves in Alberta. Wildlife management planning series No. 4. Fish and Wildlife Division, Alberta Forestry, Lands, and Wildlife. Edmonton, Alberta, Canada.
- Gunson, J. R. 1992. Historical and present management of wolves in Alberta. *Wildlife Society Bulletin* 20: 330–339.
- Harper, E. K., W. J. Paul, and L. D. Mech. 2005. Causes of wolf depredation increase in Minnesota from 1979-1998. *Wildlife Society Bulletin* 33: 889–896.
- 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 Monograph* 153: 1–35.
- Kellner, J. B., I. Tetreault, S. D. Gaines, and R. M. Nisbet. 2007. Fishing the line near marine reserves in single and multispecies fisheries. *Ecological Applications* 17: 1039–1054.
- Latham, A. D. 2008. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta. Dissertation, University of Alberta, Edmonton, Canada.
- Ling, S., and E. J. Milner-Gulland. 2008. When does spatial structure matter in models of wildlife harvesting? *Journal of Applied Ecology* 45: 63–71.
- Martínez-Espiñeira, R. 2006. Public attitudes towards lethal coyote control. *Human Dimensions of Wildlife* 11: 89–100.
- Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations.

Conservation Biology 9: 270–278.

Mosnier, A., D. Boisjoly, R. Courtois, and J. P. Ouellet. 2008. Extensive predator use can limit the efficacy of a control program. *Journal of Wildlife Management* 72: 483–491.

National Research Council. 1997. *Wolves, bears, and their prey in Alaska: Biological and social challenges in wildlife management*. National Academy Press, Washington, D.C., USA.

Novaro, A. J., K. H. Redford, and R. E. Bodmer. 2000. Effects of hunting in source-sink systems in the neotropics. *Conservation Biology* 14: 713–721.

Packard, J. M., and L. D. Mech. 1983. Population regulation in wolves. Pages 151–174 *in* F. L. Bunnell, D. S. Eastman, and J. M. Peek, editors. *Symposium on natural regulation of wildlife populations*. Forestry Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho, USA.

Poole, K. G., and G. Mowat. 2001. *Alberta furbearer harvest data analysis*. Alberta Sustainable Resource Development, Fish and Wildlife Division. Alberta Species at Risk Report No. 31. Edmonton, Alberta, Canada.

Robichaud, C. B., and M. S. Boyce. 2009. Wolf control to protect woodland caribou. *Alberta Outdoorsmen* 11(1): 26–27.

Sirén, A., P. Hambäck, and J. Machoa. 2004. Including spatial heterogeneity and animal dispersal when evaluating hunting: a model analysis and an empirical assessment in an Amazonian community. *Conservation Biology* 18: 1315–1329.

- Statistics Canada. 2008. Table 30013: Census of Wildlife Production (Survey ID 3428). CANSIM II database, Number and value of pelts produced 1970-2006, Alberta, Canada. <<http://dc1.chass.utoronto.ca/cgi-bin/cansim2/get-Array.pl?a=30013>> . Accessed 21 October 2008.
- Treves, A., and U. Karanth. 2003. Human-carnivore conflicts and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491–1499.
- Van Ballenberghe, V. 2006. Predator control, politics, and wildlife conservation in Alaska. *Alces* 42: 1–11.
- Walters, C. J., M. Stocker, and G. Haber. 1981. Simulation and optimization models for a wolf ungulate system. Pages 317-337 *in* C. W. Fowler, and T. D. Smith, editors. *Dynamics of large mammal populations*. John Wiley & Sons, New York, New York, USA.
- Webb, N. 2008. Density, demography, and functional response of a harvested wolf population in west-central Alberta, Canada. Dissertation, University of Alberta, Edmonton, Canada.
- Webb, S. M., and M. S. Boyce. 2009. Marten fur harvests and landscape change in west-central Alberta. *Journal of Wildlife Management* 73: 894–903.
- Webb, S. M., D. J. Davidson, and M. S. Boyce. 2008. Trapper attitudes and industrial development on registered traplines in west-central Alberta. *Human Dimensions of Wildlife* 13: 115–126.
- Zar, J. 1999. *Biostatistical analysis*. Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

CHAPTER 4: WOLF CONTROL TO PROTECT WOODLAND CARIBOU

Caribou have never been abundant in Alberta, yet licensed hunts were available until 1981 and even today caribou are harvested by First Nations in northern Alberta. Woodland caribou are protected under Canada's Species at Risk Act and the species is classified as "threatened" in Alberta. One small population near Grand Cache, the Little Smoky herd, is particularly at risk, and the government of Alberta has launched a wolf-control program to prevent this genetically unique population from going extinct. Although wolf predation is the most common cause of mortality in woodland caribou, industrial development and habitat alteration are the true causes of population decline.

During winter woodland caribou depend on mature old-growth forests where they forage on the lichens that hang from branches in the trees. The Little Smoky (LSM) herd has declined rapidly over the last four decades while their winter habitats have been logged for timber and for access to extract oil and gas. Only about 80 caribou remain in the LSM today, representing an 88% decline from the late 1960s. Wolf predation is merely a symptom of an altered landscape. Old growth forests have been cleared and replaced by younger forest stands that provide good habitat for moose and deer. Increased moose and deer populations have allowed wolf numbers to increase, resulting in more wolf predation on caribou even though caribou is not their primary prey. In addition, linear features such as seismic lines and roads make wolves efficient hunters--they can travel faster using these routes to access caribou habitats.

To recover the nearly extirpated caribou herd, the Alberta government sanctioned wolf control beginning in winter 2005-2006 using helicopter gunning and strychnine poisoning. Although similar initiatives have launched avalanches of public protest elsewhere, Alberta's wolf control has received relatively little public attention seemingly because actions are justified to prevent extinction of the LSM caribou herd. Over the past four winters more than 362 wolves have been removed in the range of the LSM caribou. Each year over 60 wolves have been removed and within weeks wolves have returned to the control area from

robust wolf populations on the surrounding landscape. In addition, liberalized harvests of moose and deer were begun in fall 2006 to reduce alternative prey for wolves. All boils down to habitat; the LSM caribou range has the largest industrial footprint of any other caribou herd in Canada and development continues. It might be easy to point the finger at industry; ironically even though Alberta Sustainable Resource Development is trying to “rescue” caribou using predator control, Alberta Energy continues to approve gas wells resulting in continued loss of old-growth forest habitats for caribou.

Aerial gunning and poisoning of wolves are objectionable to the public. Once begun, wolf control must be sustained to be effective because wolf populations rebound quickly. If trappers could help to control local wolf populations, I believe this would be more acceptable than aerial gunning and poisoning. I examined provincial records of wolf harvests from registered traplines over the past 22 years. Trappers have increased the harvest of wolves in recent years with an all-time high harvest of 800 wolves recorded last year. On average, trappers harvested only 10% of the provincial wolf population between 1985 and 2006. Research on wolves suggests that sustainable harvest rates are around 30-40%. In other words, harvests of greater than 40% of the population are required to reduce wolf abundance. Few trappers catch more than 5 wolves in a season with most active traplines yielding only one or two wolves per year. In the range of the LSM caribou only about 6 wolves per year were taken by trappers. Certainly trapper harvests of wolves have not reduced wolf populations; instead the population has increased over the last two decades. I observed increases in annual wolf harvests and increases in the number of traplines where wolves have been caught, despite a decline in trapper effort over time. I concluded that registered trappers in Alberta do not have a large enough impact to control wolf abundance. To effectively reduce wolf numbers trapper effort would have to increase considerably.

Gordy Klassen, president of the Alberta Trappers Association, teaches an excellent workshop to train trappers to be more effective at killing wolves. Wolves can be difficult to trap and not all trappers are effective. Alberta’s

trapline system is not designed to target increased trapping pressure in problem areas. Trapping privileges on Crown lands are allocated to individual trappers over specific areas (registered traplines) averaging 223 km². This reduces conflict among trappers and gives individuals the responsibility to manage furbearers on their traplines. Certainly trapping does not threaten the persistence of wolves in Alberta. Indeed, trapping has a stabilizing effect on populations because harvest pressure is diffused across the landscape preventing local extirpation in some areas and underutilization in others.

I was concerned that the removal of wolves in the LSM might be compensated by other predators killing caribou, particularly calves. Both black and grizzly bears are known to prey on ungulates so I conducted a diet analysis using stable isotope methods (right out of CSI) on bear hairs to determine if bears were eating caribou. I sampled hairs from black bears and grizzly bears across the LSM but did not find any bears specializing on caribou, which might not be surprising given the scarcity of caribou. But I was surprised to discover that overall black and grizzly bears had similar food habits, contradicting the widely held notion that black bear diets focus on vegetation. I documented huge dietary variation among individual bears. The amount of terrestrial protein (from moose, elk, deer, caribou, and ants) assimilated by black bears ranged from 2% to 58% of their diets. This suggests foraging specializations among black bears in the population. From an ecological perspective our findings are important because they suggest that bears operate at several levels in the food web and play different roles in the ecosystem depending on diet.

Bears cannot be dismissed as ungulate predators. Bears with more meat in their diets tend to be larger and produce more offspring than more herbivorous bears. Bear specialization on caribou, although unlikely due to low caribou density in the LSM, is possible. Feeding patterns can be passed from mothers to offspring by learning, and if a particular specialization gives individual bears an advantage over others then the specialization might become more common over time.

Trapping is not an effective method to control large-scale wolf abundance as indicated by takes well below sustainable harvest rates. Wolf management is a sensitive issue due to divided social opinion; consequently expanded wolf-control efforts in Alberta may test the public's tolerance. Short-term wolf control can allow ungulate populations to increase but merely treats symptoms and does not address the main issue of habitat loss and habitat alteration. Habitat restoration is imperative for caribou recovery because the current industrial footprint is above the threshold that can sustain caribou. If we ever want to wean ourselves from wolf control and maintain the LSM caribou herd, many years of serious habitat restoration will be required.

Although the outlook for the LSM caribou herd is grim, there is hope if habitat issues are addressed. Since wolf control began 4 years ago caribou survival and calf recruitment have been higher than before wolf control. The rate of population decline has slowed and the caribou population appears to be stabilizing--possibly increasing. Wolf control really works, and might prevent or at least forestall the extinction of the LSM caribou herd. I wish that hunters and trappers could be part of the solution, but unless we can mobilize a substantial increase in harvests it appears that we're stuck with government wolf control to prevent the extinction of woodland caribou.

APPENDIX A- BEAR HAIR $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$ ISOTOPE VALUES

Table A-1. Mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope ratios from black and grizzly bear hair samples collected in the Little Smoky area.

Species/Sample ID	$\delta^{13}\text{C}$	SD	<i>n</i>	$\delta^{15}\text{N}$	SD	<i>n</i>
<i>Black Bear</i>						
04M1	-23.50	0.18	6	3.97	0.18	6
17M1	-23.67		2	4.69		2
23M1	-23.26		2	5.24		2
28M1	-23.67		2	4.32		2
29M1	-22.43		1	5.23		1
31M1	-22.67		1	4.95		1
37M1	-23.88	0.33	4	4.46	0.46	5
39M1	-23.78		1	4.40		1
42M1	-23.67		2	3.89		2
43M1	-23.04		1	5.47		1
44M1	-23.56		1	3.43		1
46M1	-23.04		1	4.42		1
03M2	-23.04		2	4.51		2
04M2	-23.76		1	4.18		1
09M2	-24.48	0.20	4	2.36	0.08	4
17M2	-23.08	0.25	3	4.21	0.18	3
19M2	-24.61		2	2.20		2
21M2	-23.93	0.32	7	3.96	0.23	7
24M2	-22.84	0.13	6	5.41	0.16	6
32M2	-24.25		1	2.87		1
42M2	-23.80		1	3.25		1
48M2	-22.97	0.40	3	4.48	0.58	3
04M3	-23.22		1	5.32		1
08M3	-22.89	0.46	6	4.92	0.67	6
17M3	-23.54		2	3.67		2
19M3	-23.47		2	4.20		2
24M3	-23.48		1	3.55		1
37M3	-24.02		2	4.48	0.29	3
39M3	-23.77		1	4.73		1
08M4	-23.57	0.31	4	4.17	0.37	4
15M4	-23.75		2	5.10		2
41M4	-23.76		1			1
<i>Grizzly Bear</i>						
09M1	-24.25		2	2.91		2
17M1	-23.58	0.34	5	4.88	0.34	6

APPENDIX A- BEAR HAIR $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$ ISOTOPE VALUES

Table A-1 Continued

Species/Sample ID	$\delta^{13}\text{C}$	SD	<i>n</i>	$\delta^{15}\text{N}$	SD	<i>n</i>
<i>Grizzly Bear</i>						
06M2	-24.23		1	2.13		1
41M2	-23.46		1	4.13		1
17M3	-23.49		1	4.80		1

APPENDIX B- PLANT ISOTOPE VALUES

Table B-1. Isotope values of ^{13}C and ^{15}N for plant samples collected in the Little Smoky area (values have not been corrected for fractionation).

Sample ID	Common name	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Low N plants</i>				
P022	Heart-leaved Alexanders	<i>Zizia aptera</i>	-27.88	-6.26
P033	Common bearberry	<i>Arctostaphylos uva-ursi</i>	-29.11	-5.49
P012	Buttercup	<i>Thalictrum spp</i>	-28.07	-4.42
P023	Yampa	<i>Perideridia gairdneri</i>	-28.28	-4.27
P045	Northern bedstraw	<i>Galium boreale</i>	-30.82	-4.10
P028	Labrador tea	<i>Ledum groenlandicum</i>	-27.55	-3.95
P048	Canada Goldenrod	<i>Solidago canadensis</i>	-27.78	-3.81
P016	Grass	<i>spp unknow</i>	-27.04	-3.55
P041	Wild strawberry	<i>Fragaria virginiana</i>	-27.91	-3.50
P005	Common Paintbrush	<i>Castilleja miniata</i>	-25.48	-3.26
P052	Velvet-leaved Blueberries	<i>Vaccinium myrtilloides</i>	-25.78	-3.05
<i>Medium N plants</i>				
P030	Grass		-29.64	-2.95
P027	Wild Strawberry	<i>Fragaria virginiana</i>	-27.33	-2.64
P042	Baneberry	<i>Actaea rubra</i>	-28.64	-2.63
P008	Grass		-27.99	-2.63
P015	Grass		-27.20	-2.53
P036	Alpine sweet vetch	<i>Hedysarum alpinum</i>	-26.85	-2.23
P046	Bracted Honeysuckle	<i>Lonicera involucrata</i>	-29.17	-2.20
P056	Blueberrie plant	<i>Vaccinium myrtilloides</i>	-26.91	-2.17
P049	Bog Cranberry	<i>Vaccinium vitis-idaea</i>	-27.44	-2.06
P021	Common dandelion	<i>Taraxacum officinale</i>	-29.55	-1.85
P043	Skunk currant	<i>Ribes glandulosum</i>	-28.95	-1.70
P035	Yellow sweet clover	<i>Melilotus officinalis</i>	-28.39	-1.67
P001	Lily	<i>Smilacina stellata</i>	-31.28	-1.60
P044	Wild red raspberry	<i>Rubus idaeus</i>	-27.12	-1.47
P025A	Cow Parsnip	<i>Heracleum lanatum</i>	-29.91	-1.41
P034	White sweet clover	<i>Melilotus alba</i>	-28.44	-1.31
P017	Common Yarrow	<i>Achillea millefolium</i>	-30.11	-1.13
P019	Clover (red and white)	<i>Trifolium spp.</i>	-29.04	-1.04
P039	Canadian milk vetch	<i>Astragalus canadensis</i>	-26.62	-0.89
P038	Perrenial sow thistle	<i>Sonchus arvensis</i>	-28.05	-0.82
P020	Tall Larkspur	<i>Delphinium glaucum</i>	-27.50	-0.75
P050	Canada Buffaloberry	<i>Shepherdia canadensis</i>	-30.00	-0.71

APPENDIX B- PLANT ISOTOPE VALUES

Table B-1 Continued

Sample ID	Common name	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Medium N plants</i>				
P040	Wild vetch	<i>Vicia americana</i>	-25.75	-0.68
P025B	Cow Parsnip	<i>Heracleum lanatum</i>	-27.19	-0.61
P037	Grass		-27.79	-0.55
P057	Huckleberry plant	<i>Vaccinium membranaceum</i>	-30.54	-0.48
P051	Five-leaved bramble	<i>Rubus pedatus</i>	-28.81	-0.10
P002	Tall Lungwort	<i>Mertensia paniculata</i>	-26.26	0.01
P053	Black huckleberry	<i>Vaccinium membranaceum</i>	-29.18	0.59
P055	Clasping twistedstalk	<i>Streptopus amplexifolius</i>	-28.28	0.80
P047	Bunchberry	<i>Cornus canadensis</i>	-26.08	0.86
P018A	Scouring rush	<i>Equisetum hyemale</i>	-25.28	1.67
P011	Grass		-29.05	2.70
P031	Grass		-28.71	2.79
P014	Bunchberry	<i>Cornus canadensis</i>	-26.59	2.83
P018B	Swamp Horsetail	<i>Equisetum fluviatile</i>	-25.74	3.25
P010	Goldeneye	<i>Viguiera dentata</i>	-27.93	3.60
P029	Water sedge	<i>Carex aquatilis</i>	-27.99	3.60
P003	Buttercup	<i>Anemone spp.</i>	-26.93	3.81
<i>High N Plants</i>				
P024	Grass		-26.59	4.11
P026	Grass		-28.15	4.38
P018C	Wood Horsetail	<i>Equisetum sylvaticum</i>	-25.98	4.61
P004	Rose	<i>Rosa acicularis</i>	-25.31	5.84
P007	Grass	<i>spp unknow</i>	-26.53	7.06
P054	Red Elderberry	<i>Sambucus racemosa</i>	-27.78	7.56
P032	Fireweed	<i>Epilobium angustifolium</i>	-26.21	7.73

APPENDIX C- MEAT ISOTOPE VALUES

Table C-1. Stable isotope values (^{13}C and ^{15}N) for all meat food sources used in the dietary mixing model (values have not been corrected for fractionation).

Sample ID	Common name	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Sample type (source)
A001	Caribou	<i>Rangifer tarandus</i>	-22.54	1.62	Muscle
C001	Caribou	<i>Rangifer tarandus</i>	-24.93	5.21	Hair
C002	Caribou	<i>Rangifer tarandus</i>	-23.88	6.36	Hair
C003	Caribou	<i>Rangifer tarandus</i>	-24.13	6.12	Hair
C004	Caribou	<i>Rangifer tarandus</i>	-24.24	5.72	Hair
C006	Caribou	<i>Rangifer tarandus</i>	-23.78	6.11	Hair
C007	Caribou	<i>Rangifer tarandus</i>	-24.16	5.64	Hair
C008	Caribou	<i>Rangifer tarandus</i>	-24.72	5.05	Hair
C009	Caribou	<i>Rangifer tarandus</i>	-24.10	7.25	Hair
C010	Caribou	<i>Rangifer tarandus</i>	-24.21	6.17	Hair
C012	Caribou	<i>Rangifer tarandus</i>	-24.17	6.08	Hair
C013	Caribou	<i>Rangifer tarandus</i>	-23.88	6.38	Hair
C014	Caribou	<i>Rangifer tarandus</i>	-24.27	6.37	Hair
C015	Caribou	<i>Rangifer tarandus</i>	-24.08	7.20	Hair
C016	Caribou	<i>Rangifer tarandus</i>	-24.92	4.22	Hair
C017	Caribou	<i>Rangifer tarandus</i>	-24.47	4.57	Hair
C018	Caribou	<i>Rangifer tarandus</i>	-25.40	3.44	Hair
C019	Caribou	<i>Rangifer tarandus</i>	-25.19	4.44	Hair
C020	Caribou	<i>Rangifer tarandus</i>	-24.53	4.42	Hair
C021	Caribou	<i>Rangifer tarandus</i>	-24.50	5.88	Hair
C022	Caribou	<i>Rangifer tarandus</i>	-24.59	3.73	Hair
C023	Caribou	<i>Rangifer tarandus</i>	-25.34	4.25	Hair
C024	Caribou	<i>Rangifer tarandus</i>	-24.77	3.50	Hair
C025	Caribou	<i>Rangifer tarandus</i>	-25.16	4.66	Hair
A002	Caribou calf*	<i>Rangifer tarandus</i>	-22.76	1.49	Muscle
A003	Elk	<i>Cervus elaphus</i>	-25.15	4.38	Muscle
A004	Elk calf	<i>Cervus elaphus</i>	-26.11	2.24	Muscle
n/a	Elk	<i>Cervus elaphus</i>	-25.60	4.80	Hair (Urton and Hobson 2005)
n/a	Elk	<i>Cervus elaphus</i>	-25.50	3.10	Muscle (Hobson et al. 2000)
n/a	Mule deer	<i>Odocoileus hemionus</i>	-26.80	3.80	Muscle (Hobson et al. 2000)

APPENDIX C- MEAT ISOTOPE VALUES

Table C-1 Continued

Sample ID	Common name	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Sample type (source)
n/a	White-tailed deer	<i>Odocoileus virginianus</i>	-25.10	4.30	Hair (Urton and Hobson 2005)
n/a	White-tailed deer	<i>Odocoileus virginianus</i>	-25.90	4.60	Muscle (Hobson et al. 2000)
n/a	Deer	<i>O. hemionus, and O. virginianus</i>	-26.50	4.50	Hair (Stotyn 2008)
A005	Ants	Formicidae	-26.31	3.39	Whole body
n/a	Ants	Formicidae	-25.50	3.80	Whole body (Hobson et al. 2000)
n/a	Moose	<i>Alces alces</i>	-25.60	3.10	Hair (Urton and Hobson 2005)
n/a	Moose	<i>Alces alces</i>	-25.90	2.60	Hair (Stotyn 2008)
n/a	Moose	<i>Alces alces</i>	-25.70	2.90	Muscle (Hobson et al. 2000)

* All other caribou calf values were generated by correcting adult caribou nitrogen values by +1.9 ‰ to represent nitrogen enrichment observed in calves (Jenkins et al. 2001).

APPENDIX C- MEAT ISOTOPE VALUES

Table D-1. Assimilated dietary proportions of seven food items for each bear sample ($n = 38$) calculated using Isosource.

Sample ID		Caribou	Caribou calf	Ungulates	Ants	Low N plants	Med N Plants	High N plants
03M2BB	\bar{x}	5.83	5.25	24.34	11.89	40.12	7.70	4.87
	<i>Min</i>	0	0	0	0	26	0	0
	<i>Max</i>	23	23	60	61	52	32	22
04M1BB	\bar{x}	3.02	2.96	13.72	8.81	39.56	22.58	9.36
	<i>Min</i>	0	0	0	0	22	0	0
	<i>Max</i>	16	15	41	44	60	51	36
04M2BB	\bar{x}	2.09	2.02	10.15	6.52	23.77	46.76	8.68
	<i>Min</i>	0	0	0	0	8	0	0
	<i>Max</i>	12	12	32	34	57	72	44
04M3BB	\bar{x}	4.19	4.04	19.50	12.10	21.29	26.86	12.01
	<i>Min</i>	0	0	0	0	1	0	0
	<i>Max</i>	22	21	56	60	45	61	43
06M2GB	\bar{x}	0.37	0.35	2.25	1.67	48.66	44.37	2.32
	<i>Min</i>	0	0	0	0	40	29	0
	<i>Max</i>	3	3	8	9	60	59	12
08M3BB	\bar{x}	9.02	5.28	26.92	11.36	35.48	7.40	4.54
	<i>Min</i>	0	0	0	0	22	0	0
	<i>Max</i>	26	25	67	66	47	30	21
08M4BB	\bar{x}	2.69	2.61	12.89	8.16	32.72	30.91	10.02
	<i>Min</i>	0	0	0	0	15	0	0
	<i>Max</i>	15	15	39	42	57	59	42
09M1GB	\bar{x}	0.46	0.44	2.66	1.93	29.59	62.25	2.67
	<i>Min</i>	0	0	0	0	19	44	0
	<i>Max</i>	3	3	10	10	43	79	14
09M2BB	\bar{x}	0.10	0.14	1.07	0.91	38.13	58.28	1.37
	<i>Min</i>	0	0	0	0	31	48	0
	<i>Max</i>	1	1	4	5	46	69	6
15M4BB	\bar{x}	1.91	2.12	9.78	6.85	7.80	57.86	13.67
	<i>Min</i>	0	0	0	0	0	7	0
	<i>Max</i>	12	13	33	37	44	75	49

APPENDIX D- ISOSOURCE DIET RECONSTRUCTION

Table D-1 Continued

Sample ID		Caribou	Caribou calf	Ungulates	Ants	Low N plants	Med N Plants	High N plants
17M1BB	\bar{x}	2.46	2.38	11.85	7.55	16.51	49.23	10.02
	<i>Min</i>	0	0	0	0	0	0	0
	<i>Max</i>	14	14	37	39	52	76	49
17M1GB	\bar{x}	2.77	2.67	13.09	8.51	16.66	45.13	11.17
	<i>Min</i>	0	0	0	0	0	0	0
	<i>Max</i>	16	15	41	44	50	74	51
17M2BB	\bar{x}	5.89	5.14	23.58	10.71	44.44	6.24	3.99
	<i>Min</i>	0	0	0	0	32	0	0
	<i>Max</i>	22	22	58	57	55	28	20
17M3BB	\bar{x}	2.79	2.69	13.25	8.30	44.23	20.23	8.51
	<i>Min</i>	0	0	0	0	28	0	0
	<i>Max</i>	14	15	39	42	62	46	33
17M3GB	\bar{x}	3.06	2.96	14.54	9.17	22.35	36.47	11.45
	<i>Min</i>	0	0	0	0	3	0	0
	<i>Max</i>	17	16	44	47	51	68	48
19M2BB	\bar{x}	0.08	0.10	0.96	0.84	41.92	54.85	1.24
	<i>Min</i>	0	0	0	0	36	47	0
	<i>Max</i>	1	1	4	4	48	64	6
19M3BB	\bar{x}	3.09	2.99	14.64	9.16	35.80	24.45	9.88
	<i>Min</i>	0	0	0	0	18	0	0
	<i>Max</i>	17	16	43	46	56	53	37
21M2BB	\bar{x}	1.55	1.49	7.69	5.02	20.48	57.04	6.72
	<i>Min</i>	0	0	0	0	6	15	0
	<i>Max</i>	9	9	25	27	50	80	35
23M1BB	\bar{x}	5.50	3.82	17.63	10.79	20.94	29.70	11.57
	<i>Min</i>	0	0	0	0	1	0	0
	<i>Max</i>	21	20	49	58	48	62	45
24M2BB	\bar{x}	8.92	5.69	27.38	12.76	28.13	10.79	6.34
	<i>Min</i>	0	0	0	0	13	0	0
	<i>Max</i>	27	27	67	73	42	37	26

APPENDIX D- ISOSOURCE DIET RECONSTRUCTION

Table D-1 Continued

Sample ID		Caribou	Caribou calf	Ungulates	Ants	Low N plants	Med N Plants	High N plants
24M3BB	\bar{x}	3.09	2.96	14.47	8.85	48.27	14.98	7.37
	<i>Min</i>	0	0	0	0	33	0	0
	<i>Max</i>	16	15	41	44	63	40	28
28M1BB	\bar{x}	2.39	2.31	11.51	7.34	24.94	41.83	9.68
	<i>Min</i>	0	0	0	0	8	0	0
	<i>Max</i>	14	13	36	38	56	69	45
28M4BB	\bar{x}	3.65	3.78	17.62	11.48	13.02	35.89	14.55
	<i>Min</i>	0	0	0	0	0	0	0
	<i>Max</i>	21	20	53	57	42	64	52
29M1BB	\bar{x}	3.30	3.23	15.72	9.94	15.61	39.70	12.50
	<i>Min</i>	0	0	0	0	0	0	0
	<i>Max</i>	18	18	47	51	47	69	52
31M1BB	\bar{x}	13.08	7.04	31.11	6.59	38.05	2.49	1.63
	<i>Min</i>	0	0	13	0	30	0	0
	<i>Max</i>	29	27	67	40	46	16	11
32M2BB	\bar{x}	0.45	0.43	2.63	1.91	30.53	61.40	2.65
	<i>Min</i>	0	0	0	0	20	43	0
	<i>Max</i>	3	3	10	10	44	78	14
37M1BB	\bar{x}	1.79	1.74	8.81	5.72	11.52	62.75	7.67
	<i>Min</i>	0	0	0	0	0	16	0
	<i>Max</i>	11	10	28	30	45	84	40
37M3BB	\bar{x}	1.29	1.35	6.70	4.64	6.06	72.52	7.44
	<i>Min</i>	0	0	0	0	0	36	0
	<i>Max</i>	9	8	23	24	32	86	32
39M1BB	\bar{x}	2.08	2.01	10.09	6.49	17.74	52.95	8.64
	<i>Min</i>	0	0	0	0	2	1	0
	<i>Max</i>	12	12	32	34	55	78	45
39M3BB	\bar{x}	2.28	2.21	9.88	6.90	11.15	58.21	9.37
	<i>Min</i>	0	0	0	0	0	5	0
	<i>Max</i>	13	12	33	35	49	80	47
41M2GB	\bar{x}	3.13	3.03	14.82	9.25	37.54	22.67	9.57
	<i>Min</i>	0	0	0	0	20	0	0
	<i>Max</i>	17	16	43	46	57	51	36

APPENDIX D- ISOSOURCE DIET RECONSTRUCTION

Table D-1 Continued

Sample ID		Caribou	Caribou calf	Ungulates	Ants	Low N plants	Med N Plants	High N plants
41M4BB	\bar{x}	1.99	1.93	9.73	6.27	34.04	37.72	8.30
	<i>Min</i>	0	0	0	0	18	0	0
	<i>Max</i>	12	11	31	33	62	63	39
42M1BB	\bar{x}	2.31	2.24	11.15	7.12	34.60	33.42	9.16
	<i>Min</i>	0	0	0	0	18	0	0
	<i>Max</i>	13	13	35	37	60	60	41
42M2BB	\bar{x}	6.92	5.79	26.05	10.62	41.65	5.43	3.54
	<i>Min</i>	0	0	0	0	30	0	0
	<i>Max</i>	24	24	62	61	52	26	18
43M1BB	\bar{x}	4.47	5.24	21.46	14.76	23.26	18.75	10.12
	<i>Min</i>	0	0	0	0	4	0	0
	<i>Max</i>	24	24	60	68	43	52	36
44M1BB	\bar{x}	2.71	2.61	12.85	8.02	48.39	17.65	7.77
	<i>Min</i>	0	0	0	0	33	0	0
	<i>Max</i>	13	14	38	40	64	43	30
46M1BB	\bar{x}	6.00	5.31	24.42	11.40	41.61	6.87	4.39
	<i>Min</i>	0	0	0	0	28	0	0
	<i>Max</i>	23	23	60	60	53	30	21
48M2BB	\bar{x}	6.92	5.79	26.05	10.62	41.64	5.42	3.54
	<i>Min</i>	0	0	0	0	30	0	0
	<i>Max</i>	24	24	62	61	52	26	18

APPENDIX D- ISOSOURCE DIET RECONSTRUCTION

The isotope method explored in this study failed to identify the relative importance of caribou in bear diets due to confounding effect of other ungulate species. My approach however used only heavy isotopes of carbon and nitrogen, the most commonly used elements in isotope analyses. Using additional isotopes or exploring alternative methods could enable the differentiation between meat sources. For example it is possible to measure stable-isotope ratios of hydrogen (^2H), oxygen (^{18}O), and sulfur (^{34}S) (Robbins et al. 2004). Hydrogen isotopic ratios are related to trophic position in terrestrial consumers as ratios grow with increasing trophic levels (Birchall et al. 2005, Reynard and Hedges 2008). Variation in oxygen isotopes has been linked to differences in diet, water economy, and physiology (Kohn et al. 1996, Smith et al. 2002). Sulfur isotopes have been used in dietary reconstruction studies (e.g. Felicetti et al. 2003); however, studies using sulfur have largely been applied to quantify the use of marine food sources and habitats (Hobson et al. 1997, Hoekstra et al. 2002, Lott et al. 2003, Hebert et al. 2008). The use of sulfur isotopes may be particularly advantageous in answering questions surrounding caribou because of their unique dietary reliance on lichen (Edmonds and Bloomfield 1984). Epiphytic lichens are known to take up atmospheric sulfur (Krouse 1977) thus their isotopic ratios are similar to those of sulfur dioxide in the atmosphere (Wiseman and Wadleigh 2002, Zhao et al. 2003). It has been demonstrated that other plants (wheat grain and straw) have similar $\delta^{34}\text{S}$ values to those in soil sulfates indicating that sulfur uptake in plants, unlike lichen, is predominantly from the soil (Mayer et al. 1995,

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Novák et al. 2000, Alewell and Novak 2001, Zhao et al. 2003). Studies conducted in west-central Alberta confirm that elevated atmospheric $\delta^{34}\text{S}$ values are associated with sour gas plants in the area and that atmospheric $\delta^{34}\text{S}$ values were mirrored in lichens and mosses (Krouse 1977, Winner et al. 1978). Soil sulfates on the other hand are generally depleted in $\delta^{34}\text{S}$ compared to organic sulfur (Zhao et al. 2003) therefore lichen often exhibit higher $\delta^{34}\text{S}$ than other plants. This would presumably hold true in my study area due to the exposure to natural gas wells. Similarly, I would expect caribou to possess unique $\delta^{34}\text{S}$ values reflective of lichen signatures.

The use of additional isotopes would also increase the mixing model's accuracy in predicting diets (Felicetti et al. 2003, Mowat and Heard 2006). This is particularly relevant for measuring diets of omnivorous and generalist species such as bears because so many food sources can be incorporated into the mixing model. Each additional food source input into mixing models can increase the potential dietary solutions by orders of magnitude. Adding isotopes that further differentiate food sources would narrow the range of each source contribution and paint a more realist picture of the animal's actual diet.

Alternatively, other methods have been used to quantify animal diets such as sodium flux, mercury concentrations, and fatty acid analysis. Farley and Robbins (1997) suggested that the use of ^{22}Na can be useful in estimating bear food intake using the relationship between sodium intake and sodium excretion.

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This method would be challenging to apply under field conditions because it requires multiple recaptures in a short time period. It is possible to calculate kilograms of food consumed per day though this becomes increasingly complex for omnivores (Green 1978). Studying sodium fluxes would be best applied to populations known to consume primarily meat diets (Robbins and Farley 1997), and would be more useful in answering bioenergetic questions rather than quantifying one specific food source (Green 1978, Green et al. 1984).

Mercury analysis has been applied to quantify the amount of cutthroat trout in Yellowstone grizzly bears (Felicetti et al. 2004). Mercury is frequently bioaccumulated in aquatic systems (Ben-David et al. 2001) giving fish much higher mercury concentrations than terrestrial food sources. Cutthroat trout in Yellowstone had 508 ppb mercury whereas all other terrestrial foods had ≤ 6 ppb mercury (Felicetti et al. 2004). The use of mercury analysis could be applicable to determine the amount of caribou in bear diets under certain circumstances. Lichen is known to absorb environmental heavy metals and mercury uptake in particular is from atmospheric sources (Garty 2001, Poissant et al. 2008). Lichen and mosses have been shown to accumulate mercury and thus have higher mercury concentrations than other plants (Zhang et al. 1995, Evans and Hutchinson 1996, Poissant et al. 2008). Mercury in vegetation can be transferred to other biota (Poissant et al. 2008) making caribou particularly vulnerable to mercury accumulation due to their dietary reliance on lichen. Elevated levels of mercury in caribou have been documented and linked to lichen foraging (Aastrup

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et al. 2000, Larter and Nagy 2000). There is evidence that mercury concentrations in caribou are higher than in other ungulates, for example caribou in the Yukon have an average mercury concentration 20 times that of moose (Gamberg et al. 2005). Mercury analysis could potentially quantify amount of caribou in bear diets if: (1) bears have negligible inputs from aquatic systems, and (2) caribou exhibit higher mercury concentrations than other terrestrial food sources.

Fatty acid analysis is a relatively new technique that has been applied to study individual animal diets. The method is based on the principle that fatty acids are deposited in a consumer's fat stores with little or no modification therefore the diversity and frequency of fatty acid composition in fat stores creates a unique signature that can allow the identification of prey (Thiemann 2008). The method has been applied to black bears (Iverson et al. 2001); however, it has been used more extensively with polar bears (Thiemann 2008). Polar bear diets have been successfully quantified using fatty acids (Thiemann et al. 2008) because their food sources differed in fatty acid signatures (Thiemann et al. 2007). The effectiveness of this technique to study terrestrial bears is uncertain given that the diversity of fatty acids in marine systems is far greater than that of terrestrial systems and that polar bears are generally part of simpler food webs (Thiemann 2008). The technique could be used in a terrestrial setting only if the prey of interest, in my case caribou, would possess a unique fatty acid that would differentiate it from other prey species. Although this method could potentially hold some promise, the sampling procedure is relatively invasive (requires fat biopsies, milk samples,

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or blood samples) and the technique is most suited for high fat diets, therefore would best applied to study bear populations with large salmon intakes (Thiemann 2008).

Literature Cited

- Aastrup, P., F. Riget, R. Dietz, and G. Asmund. 2000. Lead, zinc, cadmium, mercury, selenium and copper in Greenland caribou and reindeer (*Rangifer tarandus*). *The Science of the Total Environment* 245: 149–159.
- Alewell, C., and M. Novak. 2001. Spotting zones of dissimilatory sulfate reduction in a forested catchment: the ^{34}S - ^{35}S approach. *Environmental Pollution* 112: 369–377.
- Ben-David, M., K. L. K. Duffy, G. M. Blundel, and R. T. Bowyer. 2001. Natural exposure of coastal river otters to mercury: relation to age, diet, and survival. *Environmental Toxicology and Chemistry* 20: 1986–1992.
- Birchall, J., T. C. O’Connell, T. H. E. Heaton, and R. E. M. Hedges. 2005. Hydrogen isotope ratios in animal body protein reflect trophic level. *Journal of Animal Ecology* 74: 877–881.
- Edmonds, E. J., and M. Bloomfield. 1984. A study of woodland caribou (*Rangifer tarandus caribou*) in west-central Alberta, 1979 to 1983. Alberta Energy and Natural Resources Fish and Wildlife Division.
- Evans, C. A., and T. C. Hutchinson. 1996. Mercury accumulation in transplanted moss and lichens at high elevation sites in Quebec. *Water, Air and Soil*

**APPENDIX E- ALTERNATIVE METHODS TO IDENTIFY CARIBOU
IN BEAR DIETS**

Pollution 90: 475–488.

Farley, S. D., and C. T. Robbins. 1997. Validation of ^{22}Na to estimate food intake of bears. *Journal of Wildlife Management* 61: 52–56.

Felicetti, L. A., C. C. Schwartz, R. O. Rye, M. A. Haroldson, K. A. Gunther, D. L. Phillips, and C. T. Robbins. 2003. Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. *Canadian Journal of Zoology* 81: 763–770.

Felicetti, L. A., C. C. Schwartz, R. O. Rye, K. A. Gunther, J. G. Crock, M. A. Haroldson, L. Waits, and C. T. Robbins. 2004. Use of naturally occurring mercury to Determine the importance of cutthroat trout to Yellowstone grizzly bears. *Canadian Journal of Zoology* 82: 493–501.

Gamberg, M., B. Braune, E. Davey, B. Elkin, P. F. Hoekstra, D. Kennedy, C. Macdonald, D. Muir, A. Nirwal, M. Wayland, and B. Zeeb. 2005. Spatial and temporal trends of contaminants in terrestrial biota from the Canadian Arctic. *Science of the Total Environment* 351–352: 148–164.

Garty, J. 2001. Biomonitoring atmospheric heavy metals with lichens: theory and application. *Critical Reviews in Plant Sciences* 20: 309–371.

Green, B. 1978. Estimation of food consumption in the dingo, *Canis familiaris dingo*, by means of ^{22}Na turnover. *Ecology* 59: 207–210.

Green, B., J. Anderson, and T. Whateley. 1984. Water and sodium turnover and estimated food consumption in free-living lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). *Journal of Mammalogy* 65: 593–599.

**APPENDIX E- ALTERNATIVE METHODS TO IDENTIFY CARIBOU
IN BEAR DIETS**

- Hebert, C. E., M. B. Bur, D. Sherman, and J. L. Shutt. 2008. Sulfur isotopes link overwinter habitat use and breeding condition in double-crested cormorants. *Ecological Applications* 18: 561–567.
- Hobson, K., K. D. Hughes, and P. J. Ewins. 1997. Using stable isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to Great Lakes contaminants research. *The Auk* 114: 467–478.
- Hoekstra, P. F., L. A. Dehn, J. C. George, K. R. Solomon, D. C. G. Muir, and T. M. O'Hara. 2002. Trophic ecology of bowhead whales (*Balaena mysticetus*) compared with that of other arctic marine biota as interpreted from carbon-, nitrogen-, and sulfur-isotope signatures. *Canadian Journal of Zoology* 80: 223–231.
- Iverson, S. J., J. E. McDonald, Jr., and L. K. Smith. 2001. Changes in the diet of free-ranging black bears in years of contrasting food availability revealed through milk fatty acids. *Canadian Journal of Zoology* 79: 2268–2279.
- Kohn, M. J., M. J. Schoeninger, and J. W. Valley. 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochimica et Cosmochimica Acta* 60: 3889–3896.
- Krouse, H. R. 1977. Sulphur isotope abundance elucidate uptake of atmospheric sulphur emissions by vegetation. *Nature* 265: 45–46.
- Larter, N. C., and J. A. Nagy. 2000. A comparison of heavy metal levels in the kidneys of High Arctic and mainland caribou populations in the Northwest

**APPENDIX E- ALTERNATIVE METHODS TO IDENTIFY CARIBOU
IN BEAR DIETS**

- Territories of Canada. *The Science of the Total Environment* 246: 109–119.
- Lott, C. A., T. D. Meehan, and J. A. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. *Oecologia* 134: 505–510
- Mayer, B., K. H. Feger, A. Gieseemann, and H. J. Jager. 1995. Interpretation of sulfur cycling in two catchments in the Black Forest (Germany) using stable sulfur and oxygen isotope data. *Biogeochemistry* 30: 31–58.
- Mowat, G., and D. C. Heard. 2006. Major components of grizzly bear diet across North America. *Canadian Journal of Zoology* 84: 473–489.
- Novák, M., J. W. Kirchner, H. Groscheová, M. Havel, J. Černý, and R. Krejčí. 2000. Sulfur isotope dynamics in two Central European watersheds affected by high atmospheric deposition of SO_x. *Geochimica et Cosmochimica Acta* 64: 367–383.
- Poissant, L., H. H. Zhang, J. Canário, and P. Constant. 2008. Critical review of mercury fates and contamination in the arctic tundra ecosystem. *Science of the Total Environment* 400: 173–211.
- Reynard, L. M., and R. E. M. Hedges. 2008. Stable hydrogen isotopes of bone collagen in palaeodietary and palaeoenvironmental reconstruction. *Journal of Archeological Science* 35: 1934–1942.
- Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus*

**APPENDIX E- ALTERNATIVE METHODS TO IDENTIFY CARIBOU
IN BEAR DIETS**

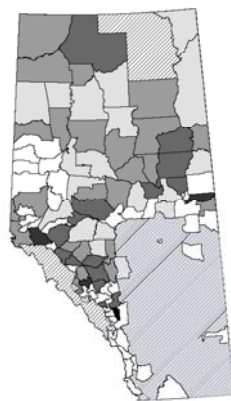
15: 161–171.

- Smith, K. F., Z. D. Sharp, and J. H. Brown. 2002. Isotopic composition of carbon and oxygen in desert fauna: investigations into the effects of diet, physiology, and seasonality. *Journal of Arid Environments* 52: 419–430.
- Thiemann, G. W. 2008. Using fatty acid signatures to study bear foraging: Technical considerations and future applications. *Ursus* 19: 59–72.
- Thiemann, G.W., S. M. Budge, S. J. Iverson, and I. Sterling. 2007. Unusual fatty acid biomarkers reveal age- and sex-specific foraging in polar bears (*Ursus maritimus*). *Canadian Journal of Zoology* 85: 505–517.
- Thiemann, G. W., S. J. Iverson, and I. Sterling. 2008. Polar bear diets and arctic marine food webs: insight from fatty acid analysis. *Ecological Monographs* 78: 591–613.
- Winner, W. E., J. D. Bewley, H. R. Krouse, and H. M. Brown. 1978. Stable sulfur isotope analysis of SO₂ pollution impact on vegetation. *Oecologia* 36: 351–361.
- Wiseman, R. D., and M. A. Wadleigh. 2002. Lichen response to changes in atmospheric sulphur: isotopic evidence. *Environmental Pollution* 116 : 235–241.
- Zhang, L., D. Planas, and J.-L. Qian. 1995. Mercury concentrations in black spruce (*Picea mariana*) and lichens in boreal Quebec, Canada. *Water, Air and Soil Pollution* 81: 153–161.
- Zhao, F. J., J. S. Knights, Z. Y. Hu, and S. P. McGrath. 2003. Stable Sulfur

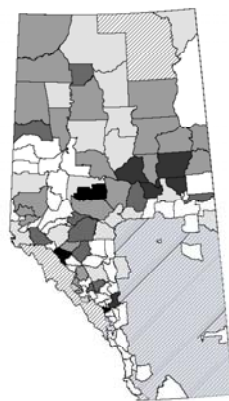
**APPENDIX E- ALTERNATIVE METHODS TO IDENTIFY CARIBOU
IN BEAR DIETS**

Isotope Ratio Indicates Long-Term Changes in Sulfur Deposition in the
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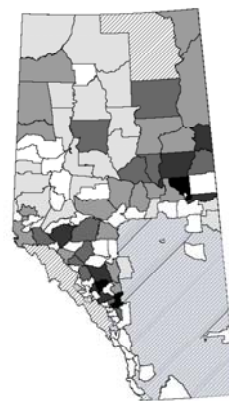
APPENDIX F- ANNUAL WOLF HARVEST MAPS



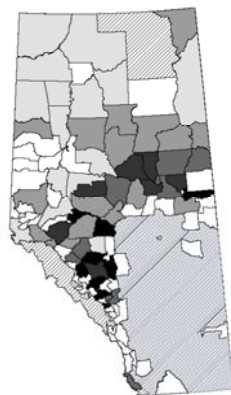
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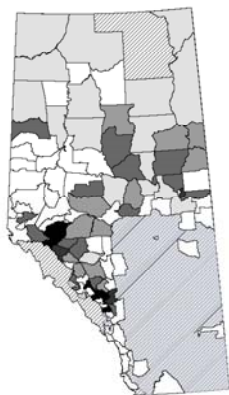
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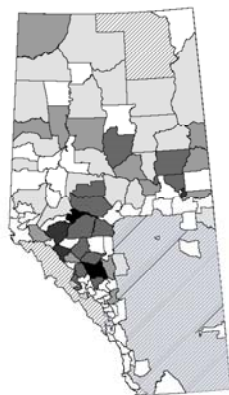
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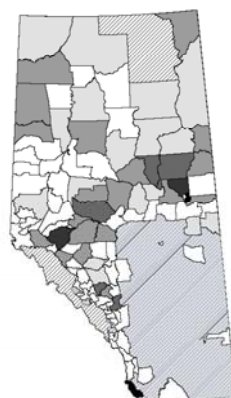
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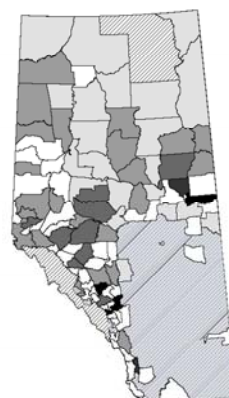
1989



1990



1991

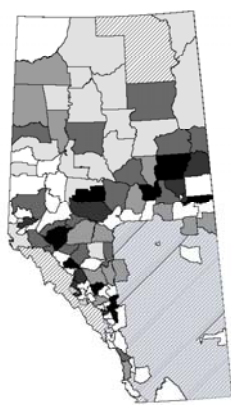


1992

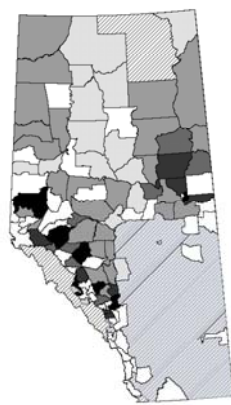
Wildlife Management Units
Wolf Harvest Classification (wolves/1000km²)

- None (0)
- ◻ Very Low (>0 to 0.5)
- ◻ Low (>0.5 to 1.5)
- ◻ Medium (>1.5 to 3.0)
- ◻ High (>3.0 to 4.5)
- ◻ Very High (>4.5)
- ▨ Private Land (no RFMA)
- ▨ National Parks (no harvest)

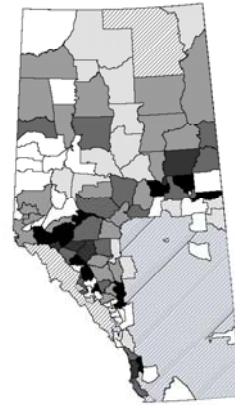
APPENDIX F- ANNUAL WOLF HARVEST MAPS



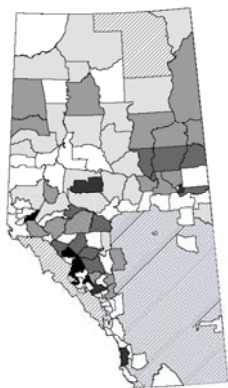
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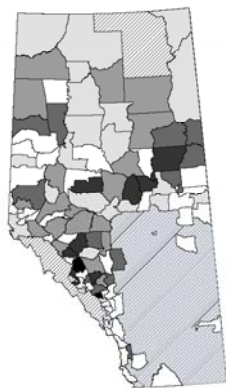
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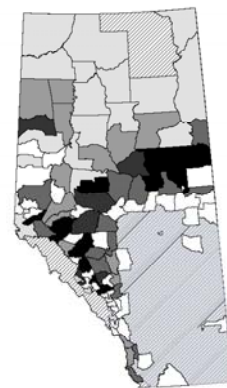
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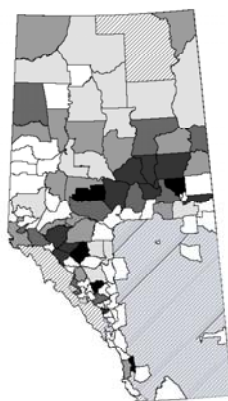
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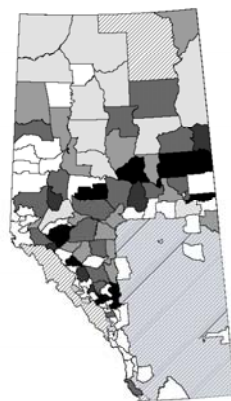
1997



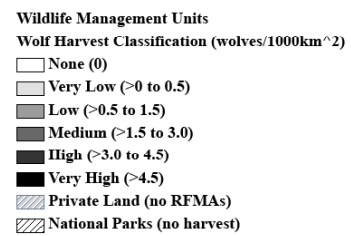
1998



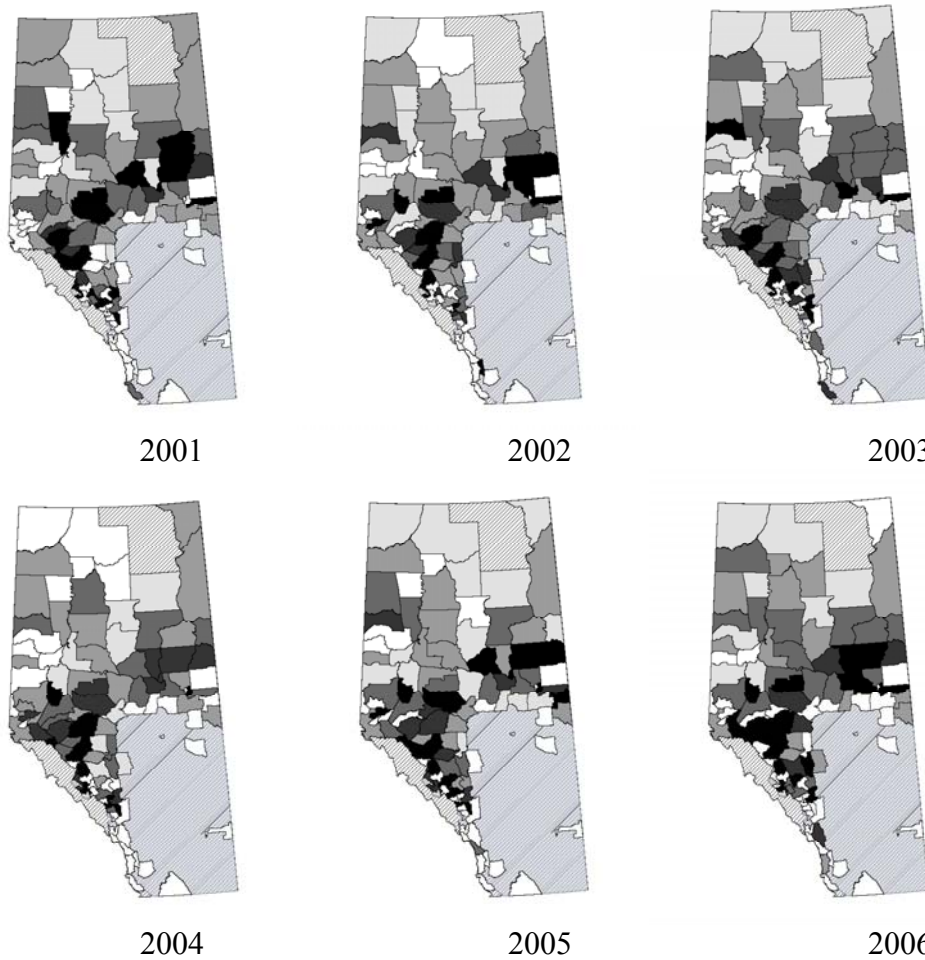
1999



2000



APPENDIX F- ANNUAL WOLF HARVEST MAPS



Wildlife Management Units

Wolf Harvest Classification (wolves/1000km²)

- None (0)
- Very Low (>0 to 0.5)
- Low (>0.5 to 1.5)
- Medium (>1.5 to 3.0)
- High (>3.0 to 4.5)
- Very High (>4.5)
- ▨ Private Land (no RFMA)
- ▩ National Parks (no harvest)