University of Alberta

The Ecology of a Re-established Cougar (*Puma concolor*) Population in southeastern Alberta and southwestern Saskatchewan

by

Michelle Margaret Bacon

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Ecology

Department of Biological Sciences

Fall 2010
Edmonton, Alberta

EXAMINING COMMITTEE

Dr. Mark S. Boyce, Department of Biological Sciences

Dr. Colleen Cassady St. Clair, Department of Biological Sciences

Dr. Naomi Krogman, Department of Rural Economy

This thesis is dedicated to my late grandmother Connie Burns,
a biologist ahead of her time,
whose ability to wear a smile in the face of great adversity
continues to inspire me, now more than ever.

ABSTRACT

Cougars (*Puma concolor*) have recently begun to reclaim former range and also are expanding into new territory. The Cypress Hills of southeast Alberta and southwest Saskatchewan now hosts the most eastern confirmed breeding population of cougars in Canada. However, with the return of cougars come new issues about human safety and risk of livestock depredation. Using GPS radiocollars, scat analysis, snowtracking and wildlife cameras, I found that the Cypress Hills boasts one of the highest densities of cougars ever reported, yet the large cats avoid human-use areas and have not been documented to prey on livestock. Using aerial ungulate survey data, I also show that the increase in cougar abundance is associated with a shift in distribution of naïve ungulate prey to areas outside the park. Provided that cougars continue to avoid humans and cattle, this island habitat could prove to be an important stepping stone to further expansion eastward.

ACKNOWLEDGEMENTS

I have many individuals and organizations to thank for contributing to the success of this project. First, I'd like to thank my supervisor, Mark Boyce, for knowing I'd be a good fit for this project and for giving me both the independence and support I needed. My graduate committee Colleen Cassady St. Clair and Naomi Krogman also provided valuable feedback and encouragement.

This project was initiated by Cypress Hills Interprovincial Park-Alberta, and the in-kind support from them was integral to our success. I'd like to express special thanks to Cameron Lockerbie of Alberta Tourism, Parks and Recreation, Cypress Hills Alberta and Saskatchewan park supervisors Julie MacDougall and Brant Seifert, and Alberta and Saskatchewan conservation officers O'Brien Tarnasky, Paul Avery, Roger Benoit, Darwyn Berndt, Jim Stock, Colin Lawson, Tanya Lawson and Jerome Schommer for their help with logistics, captures and support year-round. I am extremely grateful to the entire Cypress Hills park staff, who wholeheartedly supported me and this project from the beginning. Special thanks go to Randy Woolsey and Pius Hordos for rescuing us every time Bertha and the snowmobiles broke down!

My research would not have been possible without the financial support from Alberta Tourism, Parks and Recreation, Saskatchewan Environment, Alberta Conservation Association, Alberta Sport Recreation Parks and Wildlife Foundation, Medicine Hat Fish and Game Association, Canadian Wildlife Federation, TD Friends of the Environment, Heritage Association of Cypress Hills, Safari Club International- Northern Alberta Chapter and The Lions Club (Richmond SK and Medicine Hat AB Chapters). The Department of Biological Sciences, Faculty of Graduate Studies and Research, and Graduate Students Association at the University of Alberta provided personal financial support. I would also like to thank Alberta Tourism, Parks and Recreation, Alberta Sustainable Resource Development and Saskatchewan Environment for data sharing and collaboration.

The hard work and dedication of my volunteer field technicians was truly invaluable to the success of this project. I had the pleasure of sharing unforgettable days in the field with Greg Becic, Riley Pollom, Tyler O'Connor, Brandon Walker, Jeff Pullinger, Kurtis Plourde-Rideout, Lee Kaiser and Alex May. A special shout-out (Raaarrr!) to Jaylene Goorts, who spent 8 months in the field on "Team Coug" and lived to tell the stories.

Kyle and Aliah Knopff and Nate Webb provided assistance in captures as well as advice and encouragement throughout the project and I am so grateful that they shared their experiences with me. Lorne Hindbo- along with Poncho, Misty, Grizz, Gambler, Peg and Shorty- were enthusiastic partners in our captures. I truly enjoyed learning about cougars from Lorne, and his cheerful energy and promise of a good happy hour made winter captures that much better.

My scat lab technicians Greg Becic, Mark Epp and Martin Lankau worked hard with very little guidance, and I appreciate their commitment to a stinky job! John Taggart provided the ungulate survey data and I'm thankful for his help as well as for our many chats about wildlife. Cathy Shier, the Boyce lab coordinator, helped keep all the paperwork in order for which I am very grateful. Charlene Nielsen's expertise in GIS was incredibly helpful during analysis. Joe Northrup guided me through the world of STATA- I truly would have been lost without him, and I appreciate the time he spent helping me.

My deepest thanks go to the members of the Cougar Interest Group for their open minds, valuable feedback and positive support throughout the project. I am also extremely grateful to the ranchers and Cypress Hills' community members who allowed me on their property and shared their cougar stories with me; it was truly a pleasure getting to know you and Elkwater will always hold a special place in my heart.

I am so grateful to the members of the Boyce lab and to the friends I made while at the University of Alberta for assistance, support and fun distractions. Thanks especially to Kim Dawe, Christine Robichaud, Mara Erickson, Joe Northrup, Jesse Tigner and Lani Stinson. Andrea Morehouse, the wolf to my cougar, went through every joy and challenge of carnivore work with me. From stairway tears to Beyonce-breaks, I truly can't express how thankful I am to have had your support and friendship on this wild ride.

I was fortunate to grow up with a family that instilled in me a passion for wildlife and the great outdoors. My parents especially have always supported me throughout my adventures- I am so grateful for their gifts of roots and wings. Andrea Switzer provided me with escapes from the field, and our long talks about life helped to remind me of the big picture.

To my Elkwater family- Nic, Louis, Pius, Kaleigh, Randy, Joe, Ronnie, Courtney and Mapstone- thank you for the amazing memories we shared during the two years I spent in the field. Hockey games, campfires, rodeos, shop parties and mud-bogging helped me succeed more than you may ever realize!

Lastly, I'd like to thank Tyler O'Connor, the most unexpected surprise I found in the Cypress Hills. You have been a friend to laugh with, a shoulder to cry on, a rock of support - having you by my side throughout this journey made every day better. If the cougar project is any indication, then no doubt our future together will be full of exciting adventures- I can't wait to see what's next!

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION

BACKGROUND

Cougars (*Puma concolor*) were eradicated from much of their range in North and South America in the early part of the 20th Century due to increased agricultural development, reduced prey populations, and hunting and trapping efforts by European settlers (Figure 1). Perhaps due to their ability to adapt to most habitat types, this member of the *Felidae* family, commonly referred to as mountain lion or puma, still has the largest range of any land mammal in the Americas despite extirpation efforts throughout the continents (Currier 1983; Culver 2010).

Cougars are solitary predators that rarely interact with each other. They stalk and ambush their prey, which are primarily ungulates but can also include small mammals and birds (Hornocker 1970; Ackerman et al. 1984; Iriarte et al. 1990; Thompson et al. 2009). Individual specialization on prey by cougar has been reported (Ross et al. 1997; Festa-Bianchet et al. 2006) and can be problematic if the selected prey is endangered (Hayes et al. 2000; Rominger et al. 2004) or is domestic livestock (Palmeira et al. 2008). Males are highly territorial and can have home ranges up to and exceeding 750km^2. Their home ranges typically encompass the home ranges of several females, which vary from about 55 to 300 km^2 (Logan and Sweanor 2010). Although female territories overlap, they tend to avoid each other and some research suggests that this behaviour helps to limit population densities (Seidensticker et al. 1973; Spreadbury et al. 1996). Other studies propose that food is limiting, and thus cougar numbers would track the abundance of their primary prey (Pierce et al. 2000; Logan and Sweanor 2001; Laundré et al 2007). Because white-tailed deer (*Odocoileus virginianus*) populations are increasing in both abundance and distribution (Roseberry and Woolf 1998; Crete and Daigle 1999), it should therefore come as no surprise to see cougar populations expanding and increasing throughout the continent as well (Toweill et al. 2008).

In Canada, cougars were distributed throughout the southern part of the country, but since the early 1900s they have been limited to British Columbia and western parts of Alberta. British Columbia has an estimated 4,000 - 6,000 cougars (Austin 2003) and they persist at high densities on both the mainland and on Vancouver Island, where a subspecies of cougar (*P.c. vancouvernsis*) with lower genetic variation has been identified (Culver et al. 2000; Wilson et al. 2004). In Alberta, cougars were once persecuted under a bounty but in 1971 they were designated a big game species. A quota system for hunting with hounds occurs from December to February in many western management units. The provincial government sets separate harvest quotas for males and females, and the unit is closed to cougar hunting when either quota is met (Alberta Sustainable Resource Development 2007). The last province-wide study in 1992 estimated a population of approximately 700 cougars (Ross et al. 1996; Gunson 1997); currently, the provincial population estimate is a conservative 1,200 (J. Allen, Alberta Sustainable Resource Development, personal communication). In Saskatchewan, cougars are listed as a protected species and the current population estimate is less than 300 individuals. However, a documented increase in sightings across the province during the past decade indicates that those numbers are likely an underestimate (M. Gollop, Saskatchewan Environment, personal communication). Further east, cougars have made appearances in Manitoba, Ontario, Quebec and New Brunswick; in Ontario, sightings have occurred throughout the province and they have been listed under the province's Endangered Species Act (Ontario Puma Foundation 2010; Ontario Ministry of Natural Resources 2010).

The amazing dispersal capability of cougars is likely the catalyst for cougar expansion. Since the introduction of Global Positioning System radiocollars, dispersals by both male and female cougars of over 1,000 km have documented (Thompson and Jenks 2005; Stoner et al. 2008). Along with their tendency to be solitary and crepuscular (Beier et al. 1995; Sweanor and Logan 2010), their aptitude for long-distance dispersal has allowed cougars the opportunity to traverse long distances during times when encounters with humans are unlikely, and have increased their opportunities to successfully re-establish in new or former habitats. Now, because their current habitats are both naturally and artificially fragmented, cougars likely exhibit metapopulation status (Hanski 1998) throughout much of their range (Sweanor et al. 2000; Stoner et al. 2006). If this is so, small forest patches throughout the prairie provinces and states can act as stepping stones, making expansion to more distant populations in eastern North America possible.

CONFLICT BETWEEN HUMANS AND PREDATORS

Predators provoke emotional responses by humans, especially when their presence is due to a recent establishment, either naturally or through reintroduction programs (Hamilton 2006). Although human emotions towards predators range from awe to hatred, biologists' understanding of the important role of large carnivores in an ecosystem is increasing. Studies in Yellowstone National Park and Zion National Park have shown the consequences that the lack of a top carnivore (wolves (*Canis lupus*) and cougars, respectively) can have on an ecosystem by allowing a high-density ungulate population to persist with herbivory limiting native vegetation (Ripple and Beschta 2006a; 2006b). Likewise, those studies also have indicated that the relocation and re-colonization of carnivores into an area can have a rapid effect on re-storing the system to balance (Beschta and Ripple 2009).

In spite of the ecological benefits, large carnivores also can have damaging effects on prey populations. Predation by wolves has led to a global decline of caribou (*Rangifer tarandus*) throughout their northern range (Wittmer et al. 2005; Vors and Boyce 2009). Bighorn sheep (*Ovis canadensis*) in the Sierra Nevada and Peninsular ranges of California were listed as an endangered species after cougar predation led to a severe decrease in population sizes, and a cougar removal program was initiated by the government in an attempt to reverse the decline (Hayes et al. 2000). In addition, unsuccessful attempts to translocate bighorns into New Mexico were largely attributed to cougar predation (Rominger et al. 2004). Coyote (*Canis latrans*) predation on smaller mesopredators appears to be the primary cause of population declines of both kit foxes (*Vulpes macrotis mutica*) and swift foxes *(Vulpes velox*) throughout the southwestern United States (Ralls and White 1995; Karki et al. 2007).

Concomitantly, cougar attacks on humans are increasing. Since 1991, 99 attacks resulting in 12 deaths have been documented in North America, a remarkable increase compared to the number of attacks in the previous 100 years (Beier 1991; Sweanor and Logan 2010; Cougar Info 2010). The unpredictable nature of cougar attacks, along with publicity surrounding attacks, have likely contributed to increased public apprehension about the risks posed by cougars, but there is no doubt that encounters with humans are on the rise (Glavin 2004). Wolves pose a different type of threat to human livelihood through their tendency to kill livestock; in southwestern Alberta, cattle made up nearly 50% of wolf diet during the 2008 and 2009 grazing seasons (Morehouse and Boyce 2009). The risk of livestock depredation resulted in delayed wolf reintroduction into the Yellowstone region of the United States until the Defenders of Wildlife initiated the Wolf Compensation Trust to try to lessen some of the political opposition to wolf recovery (Fischer 1982; Fritts et al. 1997). Coyotes, with a reputation for killing domestic sheep, also have a historically negative relationship with ranchers that persists today (Knowlton et al. 1999; Berger 2006).

The potential risks to human life and livelihood have influenced attitudes towards carnivores, yet the value we place on wildlife and wild spaces has changed during the past several decades. Today, there is increased interest in preserving species, and the mere existence of large carnivores has value for some

(Kellert et al. 1996). However, rural communities still suffer livestock losses, and suburban neighborhoods that are encroaching onto wilderness areas are experiencing increased encounters with cougars and bears (*Ursus americanus*). We now struggle with conflicting values: a desire for safety, an interest in preserving charismatic wildlife, and the need to sustain keystone predators for the health of an ecosystem. This conflicted relationship between humans and wildlife plays an important role in decision-making processes by government officials (Kellert and Smith 2001). This is particularly true in regions that have existed without predators for many generations, and where lack of knowledge often translates into limited tolerance for these species.

COUGARS IN CYPRESS HILLS INTERPROVINCIAL PARK

The Cypress Hills of eastern Alberta and western Saskatchewan (49°40´N, 110°15´W; Figure 2) now hosts the most easterly confirmed breeding population of cougars in Canada. This unique geographical region of approximately 2,600km^2 was left intact in the last ice age, resulting in a plateau rising above the flat prairie terrain. Aboriginal peoples used the Cypress Hills as resting grounds during their annual movements between hunting grounds, and archeological evidence suggests the area was occupied by Native groups as early as 10,000 B.C. The Prairie Cree, Dakota, Assiniboin, Gros Ventre, Blackfoot, Plains Ojibwa and Crow tribes all occupied the area by the 1700s; Metis and Euro-Canadians arrived in the mid- to late 1800s (Hildebrant and Hubner 1994).

In the 1870s, the North-West Mounted Police established Fort Walsh to stop the illegal whisky trade, and cattle ranching was introduced to the area soon after (Hildebrant and Hubner 1994). Today, cattle graze year-round on private property in the region, and grazing leases inside the protected park have been allocated to community livestock associations since the late 1800s (L. Weekes, Cypress Hills Interprovincial Park-Alberta, personal communication). Although the agricultural industry employs the highest percentage of labour force in the region, the proportion of residents in agriculture is decreasing, from 19% in 1996 to 17.5% in 2001 to 14.1% in 2006 (Alberta Treasury 1999; Alberta Finance 2004; Alberta Finance, Economics and Statistics 2008). This is despite the population growth that has occurred in Cypress County, from 30,445 residents in 1996 to 36,270 in 2006 (Alberta Finance, Economics and Statistics 2008).

The Cypress Hills forest reserve was established in 1906 and expanded in 1911 under the Forest Reserves and Parks Act. In 1930, the Saskatchewan center block was designated as Cypress Hills Provincial Park; Alberta followed suit in 1951 and in 1989, the Cypress Hills Interprovincial Park agreement was signed, making the 400km^2 area Canada's first interprovincial park (Cypress Hills Provincial Park 2010). Elk were reintroduced to the Cypress Hills in 1938 and since then the population has increased markedly, resulting in conflicts with the adjacent agricultural community due to their tendency to damage fences and compete with cattle. To mitigate conflicts between elk and local ranchers, an annual management hunt is conducted inside the park, the only one of its kind in

Alberta provincial parks (Hegel et al. 2009). Deer hunting occurs only on the wildlife management units adjacent to the park.

Although occasional cougar sightings occurred in the Cypress Hills throughout the last 20 years, within the past 5 years tracks and sightings have increased significantly (Table 1). In 2006, confirmation was attained when a family of 3 cougars was photographed on a wildlife camera set up inside the park (Figure 3), and another family of 3 was snared outside the park boundary. Having likely arrived via coulees leading from the Rocky Mountains in Alberta and/or from the Sweet Grass Hills, Bear Paw Mountains or Little Rocky Mountains in Montana—all of which are within 400km-- the cougars found an oasis of forest filled with abundant wild ungulates for the taking and no other large predators with which to compete. An isolated patch of suitable habitat that is protected from hunting, such as Cypress Hills Interprovincial Park, along with the incredible dispersal ability of cougars, may be the two ingredients needed to enable the expansion of cougar populations into the eastern parts of North America. However, the persistence of these small island populations depends largely on the human population living around the park. Regulations in both Alberta and Saskatchewan allowing private landowners to shoot cougars on their land, combined with an ingrained attitude of distrust towards carnivores (Kellert et al. 1996), might provide a challenge for cougars to persist in the prairie regions of Canada.

THESIS OVERVIEW AND OBJECTIVES

My research began in 2007 after it became apparent to wildlife managers with Alberta Tourism, Parks and Recreation that a study was needed to learn about the expanding cougar population. Alberta Parks' objectives for the research included determining the population size and density, but they also insisted that it was imperative to determine the risk to humans and livestock in the region. In this thesis, I address concerns of the many interest groups in and around the Cypress Hills by examining the ecology of this re-established cougar population.

This study is important on several scales. On a local level, Cypress Hills is a protected area with high human use in all seasons, and so public safety and education is a top priority for local residents, surrounding communities and tourists. On a regional scale, the return of carnivores to the agriculture and livestock-based ecosystem of the prairies could change the dynamics between humans and wildlife, and concern about livestock depredation is a major issue anywhere large predators exist. On a broader scope, by studying this isolated area we can gain insight into the ecological significance of habitat patches and understand how divergent interest groups can co-exist within them.

I approached this project with four specific objectives: 1) evaluate the composition and distribution of the population of cougars in Cypress Hills and the adjacent areas; 2) evaluate the seasonal and human effects on movement and range of the cougars, if any; 3) evaluate the composition of prey, including livestock, killed by cougars; and 4) evaluate the indirect effects on the behaviour of the prey, if any, since cougars re-established in the region.

I addressed these objectives through field-intensive efforts and with the use of invasive and non-invasive techniques during 2 years spent in the Cypress Hills. In Chapter 2 of this thesis, I examine the direct effects of cougar on prey. Using GPS radiocollars on 6 adult cougars, I identified clusters of points and located kill sites to determine prey selection (Anderson and Lindzey 2003; Knopff et al. 2009). To ensure accurate results, I also validated the GPS cluster method for the first time using scat analysis. I examine the indirect effects of the presence of a re-established predator in Chapter 3. I analyzed 10 years of ungulate survey data collected by Alberta Sustainable Resource Development to find a change in distribution and abundance of prey since the cougar population rebounded. I conclude with Chapter 4, where I explain the population estimate and density of cougars in the Cypress Hills after my 3-year study, and suggest management recommendations for this unique ecosystem based on my findings. Appendix A describes an incident of 6 different cougars scavenging on an elk carcass that I captured on a wildlife camera in winter 2009 in Cypress Hills-Alberta.

I am planning to submit my research findings in Chapter 2 to the *Journal of Mammalogy*, Chapter 3 to *Science*, and Appendix A to *Canadian Field Naturalist*. Each chapter is formatted according to the specific journal styles, although I have added headers to Chapter 3 for clarity in this thesis. Chapters 1 and 4 are formatted to *Journal of Mammalogy* style.

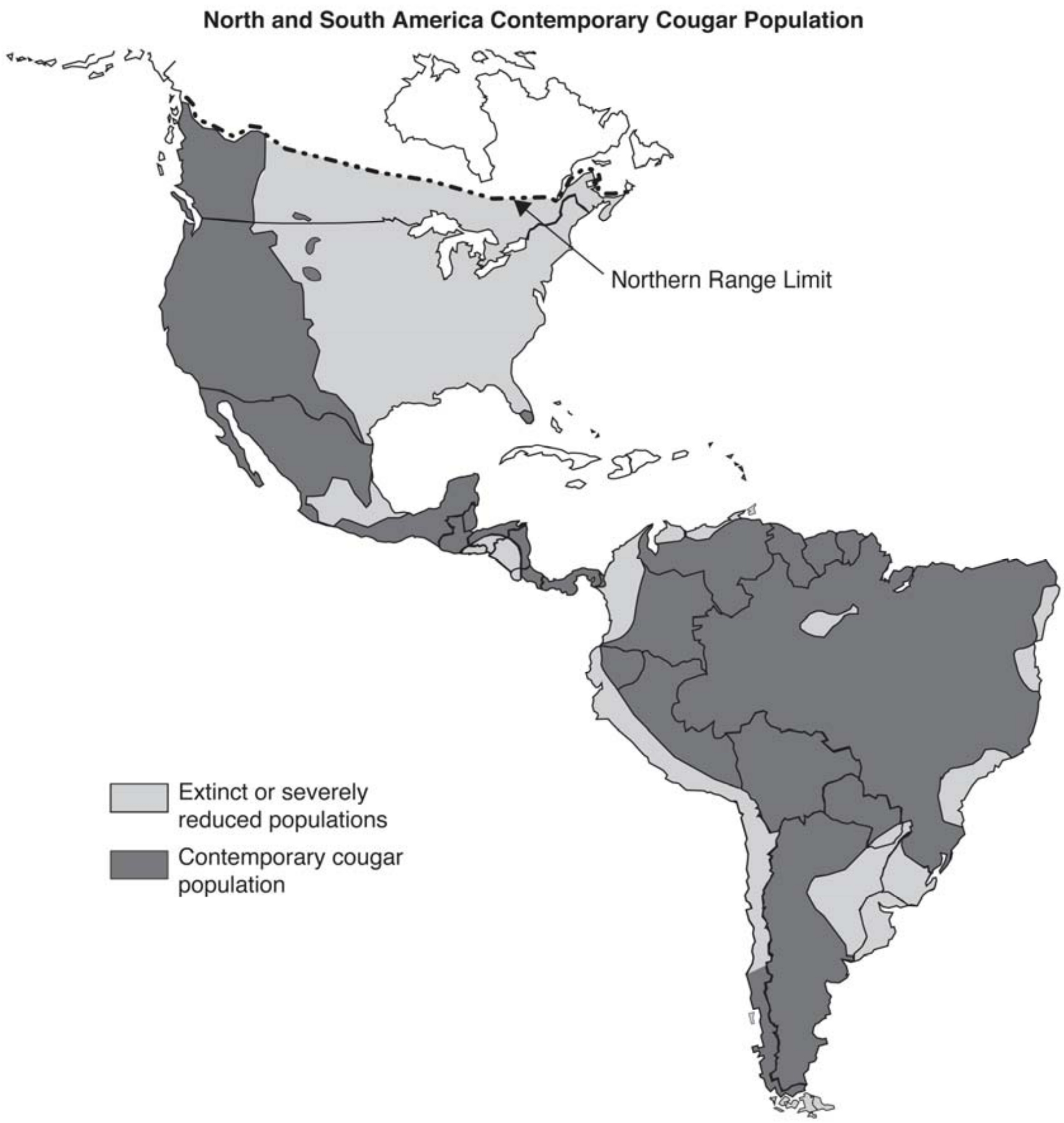

Figure 1. Historic and current range map of cougars (*Puma concolor*). Map used with permission from Cougar Ecology and Conservation, University of Chicago Press, © 2010 by Maurice Hornocker and Sharon Negri.

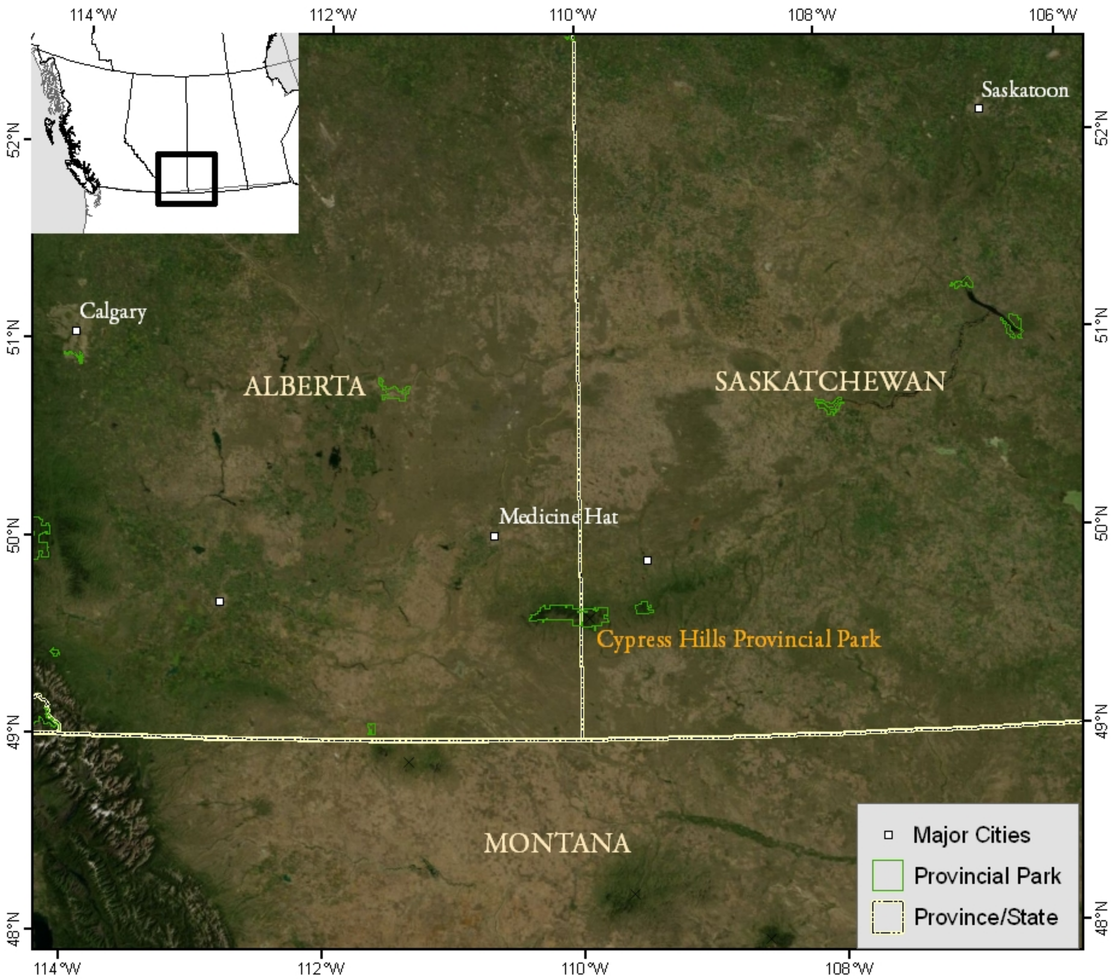

Figure 2. Location of Cypress Hills Interprovincial Park in southeast Alberta and southwest Saskatchewan, Canada.

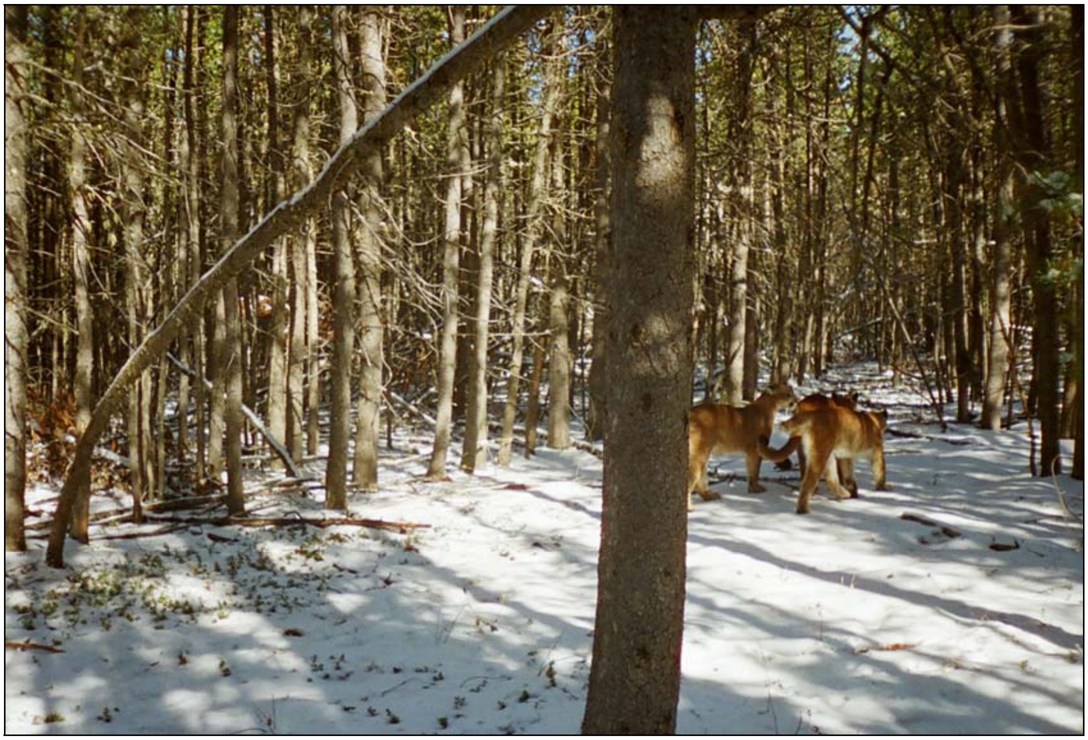

Figure 3. First image of cougars captured on a wildlife camera in Cypress Hills Interprovincial Park-Alberta, October 2006. Photo courtesy of P. Avery, CHIP-AB.

Table 1. Cougar sightings reported to conservation officers in Cypress Hills Interprovincial Park-Alberta, 2000-2009. Sightings separated by season based on human-activity levels in the provincial park.

	Pre-peak season	Peak season	Post-Peak season	Low season	
Year	May 1-June 30	July 1-Aug 30	Sept 1-Oct 10	Oct 11-April 30	Year Total
2000	1	0	0	0	1
2001	0	0	0	1	1
2002	0	0	0	3	3
2003	0	3	1	1	5
2004	1	2	1	7	11
2005	2	2	1	11	16
2006	0	2	3	8	13
2007	8	8	3	16	35
2008	2	2	1	4	9
2009	5	2	7	1	15
Total	19	21	17	52	109

LITERATURE CITED

Ackerman, B. B., F. G. Lindzey, and T. P. Hemker. 1984. Cougar food habits in Southern Utah. Journal of Wildlife Management 48:147–155.

Alberta Finance. 2004. Alberta provincial electoral profiles compiled from the 2001 Census of Canada. Government of Alberta, Edmonton, Alberta, Canada.

Alberta Finance, Economics and Statistics. 2008. Alberta provincial electoral divisions 2008 profiles. Government of Alberta, Edmonton, Alberta, Canada.

Alberta Sustainable Resource Development. 2007. Alberta Guide to Hunting Regulations. Sports Scene Publications Inc, Edmonton, Alberta, Canada.

Alberta Treasury. 1999. Alberta provincial electoral division profiles. Government of Alberta, Edmonton, Alberta, Canada.

Anderson Jr., C. R., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67:307–316.

Austin, M. 2003. Mountain lion status report: British Columbia. Page 87 i*n* S. A. Becker, D. D. Bjornlie, F. Lindzey, and D. S. Moody, eds. Proceedings of the seventh mountain lion workshop. Lander, Wyoming.

Beier, P. 1991. Cougar attacks on humans in the United States and Canada. Wildlife Society Bulletin 19:403–412.

Beier, P., D. Choate, and R. H. Barrett. 1995. Movement patterns of mountain lions during difference behaviors. Journal of Mammalogy 76: 1056–1070.

Berger, K. M. 2006. Carnivore-livestock conflicts: effects of subsidized predator control and economic correlates on the sheep industry. Conservation Biology 20:751–761.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401–2414.

Cougar Info. 2010. List of confirmed cougar attacks in the United States and Canada 2001 to now. http://www.cougarinfo.org/attacks3.htm (accessed May 28, 2010).

Crete, M., and C. Daigle. 1999. Management of indigenous North American deer at the end of the 20th Century in relation to large predators and primary production. Acta Veterinaria Hungarica 47:1–16.

Culver, M. 2010. Lessons and insights from evolution, taxonomy, and conservation genetics. Pages 27–40, *in* M. Hornocker and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, USA.

Culver, M., W. E. Johnson, J. Pecon-Slattery, and S. J. O'Brien. 2000. Genomic ancestry of the American puma (*Puma concolor*). Journal of Heredity 91:186–197.

Currier, M. J. P. 1983. Felis concolor. Mammalian Species 200:1–7.

Cypress Hills Provincial Park. 2010. Recent history and Fort Walsh. www.cypresshills.com (accessed July 27, 2010).

Festa-Bianchet, M., T. Coulson, J.- M. Gaillard, J. T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. Proceedings of the Royal Society: Biological Sciences 273:1537–1543.

Fischer, H. 1982. Restoring the wolf: Defenders launches a compensation fund. Defenders 66:34–39.

Fritts, S. H., E. E. Bangs, J. A. Fontaine, M. R. Johnson, M. K. Phillips, E. D. Koch, and J. R. Gunson. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and Central Idaho. Restoration Ecology 5:7–27.

Glavin, T. 2004. Cougar Attack! Canadian Geographic 124(3):53–66.

Gunson, J. R. 1997. Evaluation of quota hunting for cougar in Alberta during 1990-1997. Alberta Environmental Protection, Occasional Paper No. 18, Edmonton. 20pp.

Hamilton, D. 2006. Cougar hysteria: addressing mountain lion mania in the Midwest and the East. Wild Cat News 2(3):1–7.

Hanski, I. 1998. Metapopulation dynamics. Nature 296:41–49.

Hayes, C. L., E. S. Rubin, M. C. Jorgensen, R. A. Botta, and W. M. Boyce. 2000. Mountain lion predation of bighorn sheep in the Peninsular Ranges, California. Journal of Wildlife Management 64:954–959.

Hegel, T. M., C. C. Gates, and D. Eslinger. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. Journal of Environmental Management 90:222–235.

Hildebrant, W., and B. Hubner. 1994. The Cypress Hills: the land and its people. Purich Publishing, Saskatoon, SK Canada.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:3–39.

Iriarte, J. A., W. L. Franklin, W. E. Johnson, and K. H. Redford. 1990. Biogeographic variation of food habits and body size of the American puma. Oecologia 85:185–190.

Karki, S. M., E. M. Gese, and M. L. Klavetter 2007. Effects of coyote population reduction on swift fox demographics in southeastern Colorado. Journal of Wildlife Management 71:2707–2718.

Kellert, S. R., M. Black, C. Reid Rush, and A. J. Bath. 1996. Human culture and large carnivore conservation in North America. Conservation Biology 10:977−990.

Kellert, S. R., and C. P. Smith. 2001. Human values toward large mammals. Pages 30-63, *in* S. Demarias and P. Krausman, editors. Ecology and management of large mammals in North America. Prentic Hall, Upper Saddle River, New Jersey, USA.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586–597.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52:398–412.

Kulig, J. J. 1996. The glaciation of the Cypress Hills of Alberta and Saskatchewan and its regional implications. Quaternary International 32:53–77.

Laundré, J. W., L. Hernández, and S. G. Clark. 2007. Numerical and demographic responses of pumas to changes in prey abundance: testing current predictions. Journal of Wildlife Management 71:345–355.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: Evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C., USA.

Logan, K. A., and L. L. Sweanor. 2010. Behaviour and social organization of a solitary carnivore. Pages 105–117 *in* Cougar ecology and conservation. *Edited by* M. Hornocker and S. Negri, The University of Chicago Press, Chicago, USA.

Morehouse, A., and M. S. Boyce. 2009. Wolves eat cattle and we pay for the livestock loss. Alberta Outdoorsman 11(3):10–13.

Ontario Ministry of Natural Resources. 2010. Species at risk. http://www.rom.on.ca/ontario/risk.php?doc_type=fact&id=135&land=en (accessed May 28, 2010).

Ontario Puma Foundation. 2010. Sightings map. http://www.ontariopuma.ca/sightings.htm (accessed May 28, 2010).

Palmeira, F. B. L., P. G. Crawshaw Jr., C. M. Haddad, K. M. P. M. B. Ferraz, and L. M. Verdade. 2008. Cattle depredation by puma (Puma concolor) and jaguar (Panthera onca) in central-western Brazil. Biological Conservation 141:118–125.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533–1543.

Ralls, K., and P. J. White. 1995. Predation on San Joaquin kit foxes by larger canids. Journal of Mammalogy 76:723–729.

Ripple, W. J., and R. L. Beschta. 2006a. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biological Conservation 133:397–408.

Ripple, W. J., and R. L. Beschta. 2006b. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230:96–106.

Rominger, E. M., H. A. Whitlaw, D. L. Weybright, W. C. Dunn, and W. B. Ballard. 2004. The influence of mountain lion predation on bighorn sheep translocations. Journal of Wildlife Management 68:993–999.

Roseberry, J. L., and A. Woolf. 1998. Density relationships for white-tailed deer in Illinois. Wildlife Society Bulletin 26:252–258.

Ross, P. I., M. G. Jalkotzy, and J. R. Gunson. 1996. The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24:490–494.

Ross, P. I., M. G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. Canadian Journal of Zoology 74:771–775.

Seidensticker, J., M. Hornocker, W. Wiles, and J. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35. 60 pp.

Spreadbury, B. R., K. Musil, J. Musil, C. Kaisner, and J. Kovak. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 60:962–969.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.

Stoner, D. C., W. R. Rieth, M. L. Wolfe, M. B. Mecham, and A. Neville. 2008. Long-distance dispersal of a female cougar in a basin and range landscape. Journal of Wildlife Management 72:933–939.

Sweanor, L. L., and K. A. Logan. 2010. Cougar-human interactions. Pages 190-205, *in* M. Hornocker and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, USA.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics and conservation. Conservation Biology 14:798─808.

Thompson, D. J., and J. A. Jenks. 2005. Dispersal by a subadult male cougar from the Black Hills, South Dakota. Journal of Wildlife Management 69:818–820.

Thompson, D. J., D. M. Fecske, J. J. Jenks, and A. R. Jarding. 2009. Food habits of recolonizing cougars in the Dakotas: prey obtained from prairie and agricultural habitats. American Midland Naturalist 161:69–75.

Toweill, D. E., S. Nadeau, and D. Smith, editors. 2008. Proceedings of the Ninth Mountain Lion Workshop May 5-8, 2008, Sun Valley, Idaho, USA.

Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626–2633.

Wilson, S. F., A. Hahn, A. Gladders, K. M. L. Goh, and D. M. Shackleton. 2004. Morphology and population characteristics of Vancouver Island cougars, *Puma concolor vancouverensis*. Canadian Field Naturalist 118:159–163.

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.

CHAPTER 2

PREDATION BY A RE-ESTABLISHED COUGAR POPULATION: SCAT ANALYSIS VALIDES TELEMETRY METHOD

INTRODUCTION

Over the past few decades, large carnivores have re-established populations in former and new ranges, both naturally and through re-introduction programs (Fritts et al. 1997; Anderson et al. 2010). The consequences of restored predators on ecosystems are still not clear, but studies in several national parks in western United States have shown that their presence can rapidly restore the vegetation composition and biomass in ungulate-dominated ecosystems (Beschta and Ripple 2009). However, the benefits that carnivores bring to ecosystems can be countered by the complex and tumultuous relationship with the humans that inhabit the surrounding areas, where a generation of humans has not encountered large predators. Concerns arise about the perceived and real threats for human safety and livestock depredation and the impacts on wild ungulate populations (Kellert et al. 1996; Woodroffe 2000; Graham et al. 2005).

Data on prey composition are important for wildlife managers because of concerns over the extent of depredation losses (Laundré and Hernández 2010). Government officials, conservationists and private landowners use information about prey selection to make conservation and management decisions. There are ecological, economic and social impacts of the interactions between predator and prey, and so collecting data that give the best representation of diet consumed by a carnivore is vital (Kellert et al. 1996; Treves and Karanth 2003; Musiani and Paquet 2004). In southeastern Alberta and southwestern Saskatchewan, Canada, a natural re-establishment of cougars (*Puma concolor*) has been observed in a unique, forested ecosystem. Although there are large populations of wild ungulate prey--primarily elk (*Cervus elaphus*) and deer (*Odocoileus virginianus, O. hemionus*) -- the high density of cougars has led to concern about possible livestock depredation. I wanted to assess the extent to which livestock depredations might be occurring in this recently established predator population by identifying the prey composition of cougar diets.

Recent advances in Global Positioning System (GPS) technology have allowed wildlife researchers to expand their knowledge about animal behaviour (Tomkiewicz et al. 2010), including habitat selection (Boyce and McDonald 1999; Chetkiewicz and Boyce 2009), movement patterns (Merrill et al. 1998; Fortin et al. 2005; Pepin et al. 2009; Valeix et al. 2010), site fidelity (Edwards et al. 2009) and home ranges (Burdett et al. 2007; Stewart et al. 2010). GPS data from radiocollars have allowed managers to identify conservation corridors (Chetkiewicz et al. 2006), and migration routes (Nelson et al. 2004). GPS radiocollars fitted on carnivores have revolutionized researchers' ability to locate kill sites, increasing our knowledge about predation events and decreasing time in the field searching for kills (Sand et al. 2005; Franke et al. 2006; Zimmermann et al. 2007; Webb et al. 2008; Knopff et al. 2009). Models developed using GPS locations, such as those created for wolves by Sand et al. (2005) and Webb et al. (2008) and for cougars by Knopff et al. (2009), have predicted the probability of a

GPS cluster correctly identifying a predation incident as well as estimating the biomass at that kill site. These models were tested in the field and although effective, were biased towards larger prey that required long handling times. Given the frequent missing locations and habitat bias that can occur with GPS radiotelemetry (Frair et al. 2004; Hebblewhite et al. 2007), I questioned whether bias towards large kills might be just one of many problems associated with GPS telemetry clusters for identifying cougar diet composition.

To address my initial objective of characterizing prey composition, I needed to first ensure the method would provide an accurate picture of the diet of cougars. The GPS cluster technique has yet to be compared with analysis of prey detected from scat, a more traditional, albeit biased, method for analyzing wildlife diets (Reynolds and Aebishcher 1991; Litvaitis 2000). Hence, my objective was 2-fold: determine the prey composition of the re-established cougar population in the Cypress Hills, and validate methods by comparing cougar diet composition from kill sites found using GPS clusters and hair samples identified from scat samples.

MATERIALS AND METHODS

Study Area

I studied cougars in Cypress Hills Interprovincial Park, a 400km^2 protected area in southeast Alberta and southwest Saskatchewan, Canada (49°40′N, 110°15′W). Having escaped glaciation in the last ice age, this island of forest habitat rises over

500m above the surrounding prairie land, which is dominated by private livestock ranches. Four natural habitats make up the park ecosystem: montane (*Pinus contortata*, *Picea glauca*, *Populus tremuloides, Crataegus* spp., *Salix* spp.), fescue grassland (*Festuca* spp., *Danthonia* spp., *Agropyron* spp.), mixed-grass (*Agropyron* spp., *Stipa* spp.) and wetlands (Newsome and Dix 1968). A large diversity of mammal species exist in the Cypress Hills including white-tailed deer, mule deer, elk, moose (*Alces alces*), pronghorn antelope (*Antilocapra americana)*, coyotes (*Canis latrans*), marten (*Martes americana*), beavers (*Castor canadensis*), porcupines (*Erethizon dorsatum*) and ground squirrels (*Spermophilus richardsonii*). Cattle grazing occurred inside the park from June to October, and year-round on adjacent private ranches. An elk management hunt occurred each fall on both the Alberta and Saskatchewan sides of the park; deer hunting was prohibited inside park boundaries although they were hunted in the adjacent wildlife management units. Mean annual precipitation during 1987-2007 was 561.6mm and mean January and July temperatures were -9.0°C and 15.9°C, respectively (Environment Canada 2009).

Cougars, wolves (*Canis lupus*) and bears (*Ursus* spp.) were eradicated from the region in the early 1900s (Alberta Fish and Wildlife Division 1992). Sightings of cougars have occurred sporadically since the mid-1990s, and increased substantially since the early-2000s although none were confirmed until 2004 when a cougar kitten was struck and killed by a vehicle on an adjacent highway. In 2006 a wildlife camera captured a photo of a family of 3 cougars, and 3 other cougars were snared incidentally outside the park boundary. The population is now estimated to be between 15-20 adults; including kittens located with family groups in 2009, population densities are estimated to be between 6.75 and 8.5 cougars/100km^2, some of the highest ever reported (Bacon et al. 2009; Quigley and Hornocker 2010).

Kill sites

I captured 6 cougars (2 adult male, 4 adult female) during winters 2008 and 2009 using trained hounds to track and tree cougars and then administering a combination of either 2 mg/kg Xylazine and 3 mg/kg Telazol or 75ug/kg Medetomodine and 2mg/kg ketamine via remote injection (University of Alberta Animal Care Protocol no. 568802). I fitted cougars with Lotek 4400S remote-downloadable GPS collars (Lotek Engineering, Newmarket, ON, Canada), programmed to take GPS locations every 3 hours. I collected 761-2,381 GPS locations per cougar and telemetry transmitters remained active on the animals for 106-358 days. Collars had an average 83% fix success rate. I monitored cougars from April 25 2008 to December 9 2009, downloading location data from active collars about every 3 weeks from the ground. Data were then transferred into ArcGIS 9.2 (ESRI 2006, Redlands, California, USA), and following methods developed by Anderson and Lindzey (2003) and refined by Knopff et al. (2009), I identified GPS location clusters as $\geq$ 2 points within 200m within a 6 day time frame. After identifying the geometric center of each cluster, I programmed these points into handheld GPS units and field crews conducted ground searches at each cluster location. When prey remains were found at the cluster, we looked for evidence of cougar predation behaviour including a buried carcass, a bed of hair at the cache and scat piles. All remains were examined to identify species; when bones remained, we determined age and sex of the prey, and used the colour of the bone marrow to assess condition of the prey.

Scat collection and laboratory analysis

I located cougar scat several ways: at kill sites and non-kill clusters found using the cluster methods from the 6 radiocollared cougars, at kill sites found opportunistically from uncollared cougars, and opportunistically along trails in the park as well as on adjacent private land. Scat collection began in May 2008 and continued until December 2009. Scat deposited by cougar was identified based on the shape, size, and distinctive un-tapered ends. Scat were bagged and labelled with a GPS coordinate, date, time and cougar ID (9999 for unknown cougar), then stored in a -20^{o}C freezer until processing.

Following lab procedures described by Ackerman et al. (1984), scat samples were autoclaved for 90 minutes to clear the fecal material of possible parasites, then washed under warm water using a 0.455mm metal sieve to remove excess fecal material. Remaining contents such as teeth, hooves, claws and hair were air dried under a fume hood. Once dried, we randomly selected 20 guard hairs from each sample and placed them on slides which were examined under a compound microscope. We identified hair based on cuticular scales and medulla pattern (Moore et al. 1974) as well as size and colour of the hair from reference specimens in the Zoology museum at the University of Alberta. White-tailed deer and mule deer were pooled due to difficulties in distinguishing the species. Hairs from sciurids smaller than marmots were pooled with pocket gophers

(Geomyidae) and grouped as ground squirrels. Mice, shrews, and voles were pooled as small rodents. Badgers (*Taxidea taxus*) were not grouped with Mustelidae because their significantly larger size would have affected biomass calculations.

Analysis of hair from scat

Several studies have used scat to determine diet composition of carnivores (Floyd et al. 1978; Ackerman et al. 1984; Weaver 1993; Reed et al. 2006; van Dijk et al. 2007). In these studies, prey typically were analyzed using 1 of 3 methods: (1) occurrence of prey relative to total number of scats analyzed; (2) occurrence of prey relative to total number of hairs analyzed; and (3) occurrence of prey relative to total prey items identified in scat.

Although examining the occurrence of prey items or hairs in a scat sample provides a general overview of taxa consumed, these methods overestimate the amount of meat actually consumed from large mammalian prey. Hence, biomass correction factors have been modeled to approximate the amount that each prey species contributes to diet. Weaver (1993) conducted captive feeding trials with wolves and calculated a biomass correction factor $y = 0.439 + 0.08x$, where y is the weight of prey consumed per collectable scat (kg/scat) and x is mean prey body weight (kg). Ackerman et al. (1984) similarly conducted captive cougar feeding trials, after which they calculated a biomass correction factor specifically for cougar ($y = 1.98 + 0.035x$). Several steps are required to estimate the relative biomass consumed of each prey item found in scat. First, the correction factor for cougar was calculated using the estimated live weight of prey and the Ackerman et al. (1984) linear regression model. Prey items < 2kg did not have the correction factor applied to them because of the assumption that 1 small prey item would not comprise a total scat (Ackerman et al. 1984). Biomass consumed of each prey was calculated by multiplying the correction factor for that prey item by the occurrence of the given prey item relative to all prey items. Lastly, the relative biomass consumed of each prey was calculated by dividing the biomass consumed per prey item by the total biomass consumed of all prey items.

An issue that arises with the correction factor calculations is that they are based on captive feeding trials where the animal was fed only 1 prey item prior to defecating. Indeed, I found that 138 of 211 scat samples (65%) had > 1 prey item. To account for the fact that such a large percentage of scats contained more than 1 prey item, I used the occurrence of prey relative to total prey items identified in scat in my biomass calculations. This is different than methods described in Ackerman et al. (1984), who used prey items relative to scat, but similar to Reed and colleagues' study with wolves (2006). Average weight of prey was based on data from Pattie and Fisher (1999).

RESULTS

Kill sites located with GPS Clusters

I found 266 kill sites from April 2008 to December 2009 using the GPS cluster method. Nine species were represented in the kill sample (Table 1). Deer accounted for 76% and elk accounted for 15% of all located kills. I found no evidence of livestock depredation at any kill site.

Occurrence of Prey in Scat

I collected 233 scat samples, but included only 211 in the analysis due to lack of sufficient hair, lack of collection location, or possible pseudoreplication (multiple scats collected at the same location, probably deposited by the same individual). I identified 4,220 hairs and detected 409 prey items, with a wider array of species represented in the scat than among kill sites. Deer (white-tailed and mule deer combined) represented 55.4% of all hairs identified and comprised 37% of the prey items relative to all prey items identified. Elk represented 15.6% of the hairs identified and comprised 11% of the prey items. Sciuridae (mostly ground squirrel) and Geomyidae represented 11% of hairs identified and comprised 23.5% of the prey items. I found no evidence of livestock hair in any scat sample. Cougar hair represented 1% of all hairs identified in the scat (Table 1).

Distribution of Prey Items: Kills vs. Scat

Because I had insufficient sample sizes for some types of prey, I pooled carnivores (cougar and coyote) and small prey species (any prey < 10kg plus beaver) before conducting a chi square analysis on diet composition from kill sites and diet composition from scat. I found a significant difference in the distribution of occurrence of prey items found at kill sites and in scat samples ($\chi^2 = 143.4$, $df = 4$, $P < 0.001$; Fig. 1).

To determine if either method showed seasonal differences, I compared prey found in scat and at kill sites in summer and winter. I assigned scat samples to summer or winter by the date they were collected, because the majority of samples collected were <1 month old. I had 259 samples collected during summer (May to September) and 150 samples collected during winter (October to April). Kill sites were assigned to a season based on the date the GPS cluster was formed (assuming the date of cluster creation was the date of prey mortality); I located 141 kill sites in summer (May to September) and 125 kill sites in winter (October to April). I eliminated moose and carnivores from statistical analysis due to insufficient sample size, and pooled small prey < 10kg with beaver. Again, there was a statistical difference in prey composition between the two methods, both in summer ($\chi^2 = 78.92$, $df = 2$, $P < 0.001$) and in winter ($\chi^2 = 48.05$, $df = 2$, $P < 0.001$) (Fig. 2).

Lastly, I conducted an analysis restricted to ungulate prey, and compared distribution of deer, elk and moose in scat and at kill sites. There was no significant difference in the frequency of ungulate prey estimated by the two methods ($\chi^2 = 3.108$, $df = 2$, $P = 0.211$) (Fig. 3).

Biomass consumed: kill vs. scat

To determine the biomass that each prey species contributed to cougar diet, I included estimated weights of prey to compare biomass distribution for the two methods (Table 2). Based on nearly equal numbers of young of the year and adult prey found at kill sites, I used the minimum estimated weights for adult ungulates, and the average estimated weights for small mammals, presented in Pattie and Fisher (1999). Once prey were converted into relative biomass, using Ackerman et al.'s (1984) correction factor for the scat, both GPS clusters and scat analysis clearly indicated that the majority of biomass consumed came from ungulates. Small mammals found in the scat contribute < 8% to diet biomass (Fig. 4). When

I compared biomass of just the 3 ungulate prey, the consumption of biomass for the 3 species in both methods was nearly identical (Table 3).

Lastly, to detect biases in scat biomass resulting from collecting samples at kill sites, I compared prey items and biomass of scat from kill sites to scat samples found either incidentally or at clusters without kills or on trails. Again, there was no significant difference in the frequency of prey items between locations where they were collected ($\chi^2 = 1.89$, $df = 3$, $P = 0.59$) (Fig. 5).

DISCUSSION

For most large carnivores, ungulates make up the majority of their diets (Ross et al. 1997; Biswas and Sankar 2002; Gau et al. 2002; Husseman et al. 2002; Kortello et al. 2007). Using both kill site and scat analysis, I found that deer and elk clearly contributed the highest proportion of biomass consumed by cougars in the Cypress Hills. Although small mammals were detected at high frequencies, they contributed < 8% of the total biomass consumed. Large predators commonly prey on small mammals, e.g., grizzly bears have been observed to dig deep holes to gain access to ground squirrels in the Arctic (Doak et al. 2003). Small prey might be more abundant and they usually do not require the high-energy output involved in chasing and killing ungulates, but the caloric benefits are much lower than for deer or elk (Carbone et al. 2007).

Domestic livestock were not detected in scat or at kill sites. Throughout the study period, there were no confirmed livestock depredation events despite high availability, especially in the summer when cattle grazed inside the forested park. Cougar hair represented just 1% of all hairs, and was most often found in very small amounts, likely a result of grooming. However, there was one scat sample that was entirely made up of cougar hair. This sample belonged to the dominant male in the region, and might indicate an instance of infanticide or intraspecific kill (Logan and Sweanor 2001). We found no cougar remains at any kill site.

The frequency of occurrence of prey species varied significantly between the two methods being compared. Scat samples showed a higher variety of species whereas kill sites were biased towards large ungulate prey. Despite this apparent difference, I calculated a Shannon-Weaver index of diversity for prey items in scat (relative to total prey items identified in scat) of 0.895, and 0.842 for GPS cluster-located kills. This indicates that despite the differences in prey species occurrences, there is little consequence for prey diversity. The biomass calculations are what provided the real story about diet composition for cougars. Although scat contained a higher variety of prey, when converted to biomass it is evident that all non-ungulate prey items weighing < 10kg, along with beaver, contribute < 8% to the total biomass consumed. Although some of the finer details of diet composition will not be detected with data from kill sites only, these data still provide reliable information about which species contribute most to cougar diet.

A major bias associated with diet composition from kill sites relates to the amount of meat consumed by other cougars and scavengers. Previous studies in

California and Alberta have indicated that cougars are opportunistic scavengers (Bauer et al. 2005; Knopff et al. 2010). Using wildlife cameras in this same study area, I found multiple cougars scavenging on a large carcass as well as coyotes, small mammals, and birds (Appendix A). Murphy and Ruth (2010) report estimates of consumption at a kill site by a single cougar varies significantly by study and location. Thus, my estimate for deer and elk biomass consumed at kill sites may be high due to scavengers. The correction factor applied to scat analysis tries to compensate for this bias, but it too has biases because Ackerman et al. (1984)'s study used captive feeding trials, where cougars were only fed 1 prey species prior to fecal collection. Of the scat samples in my study, 65% contained hair belonging to multiple species. I tried to account for that by using the occurrence of prey items relative to total prey items in my calculations, rather than relative to total scats as Ackerman et al. (1984) did, but it is difficult to know how much meat a cougar actually consumes at a kill site before it leaves the kill or is jumped off by a conspecific.

Similar to my results, other research with wolves show comparable contrasts between prey estimated using scat versus GPS cluster-located kill sites (Morehouse and Boyce 2009; P. Knamiller, University of Alberta, unpublished data), indicating that these results are likely applicable to other carnivore studies using GPS clusters to locate kill sites. My results showed identical ranking of the top 2 prey items (deer and elk), and when occurrence and biomass of ungulates were compared, there was no significant difference between results from scat and results from GPS cluster-located kill sites. Unless wildlife managers are particularly interested in small prey, for most applications the GPS cluster method will provide managers with sufficient information about prey composition.

The benefits and challenges of scat analysis and GPS cluster methods must be considered when making the decision about which method to employ to characterize diet composition. Scat analysis is non-invasive and the associated financial costs are lower, but sample size is dependent on the biology and behaviour of the species being studied, e.g., wolf rendezvous sites allow for high sample size whereas cougars cover their scat so that they are much more difficult to find incidentally. The identification of the carnivore depositing the scat could be a challenge depending on the number of sympatric carnivores and domestic species that reside in the study area. There are also errors associated with lab technicians' abilities to correctly identify prey from scat samples (Foran et al. 1997). GPS radiocollars provide fine-scale information about habitat, movement and predation events. However, GPS telemetry studies are costly and require some type of immobilization of the animal, be it chemical or physical restraint. Telemetry technology is not foolproof, and radiocollars often miss locations, have location errors, drop-off too early or stop transmitting altogether. I have shown that both scat analysis and kill sites located using GPS clusters provide similar results for prey composition, and so researchers and managers must choose the method that will best fit their budget and time available for field work.

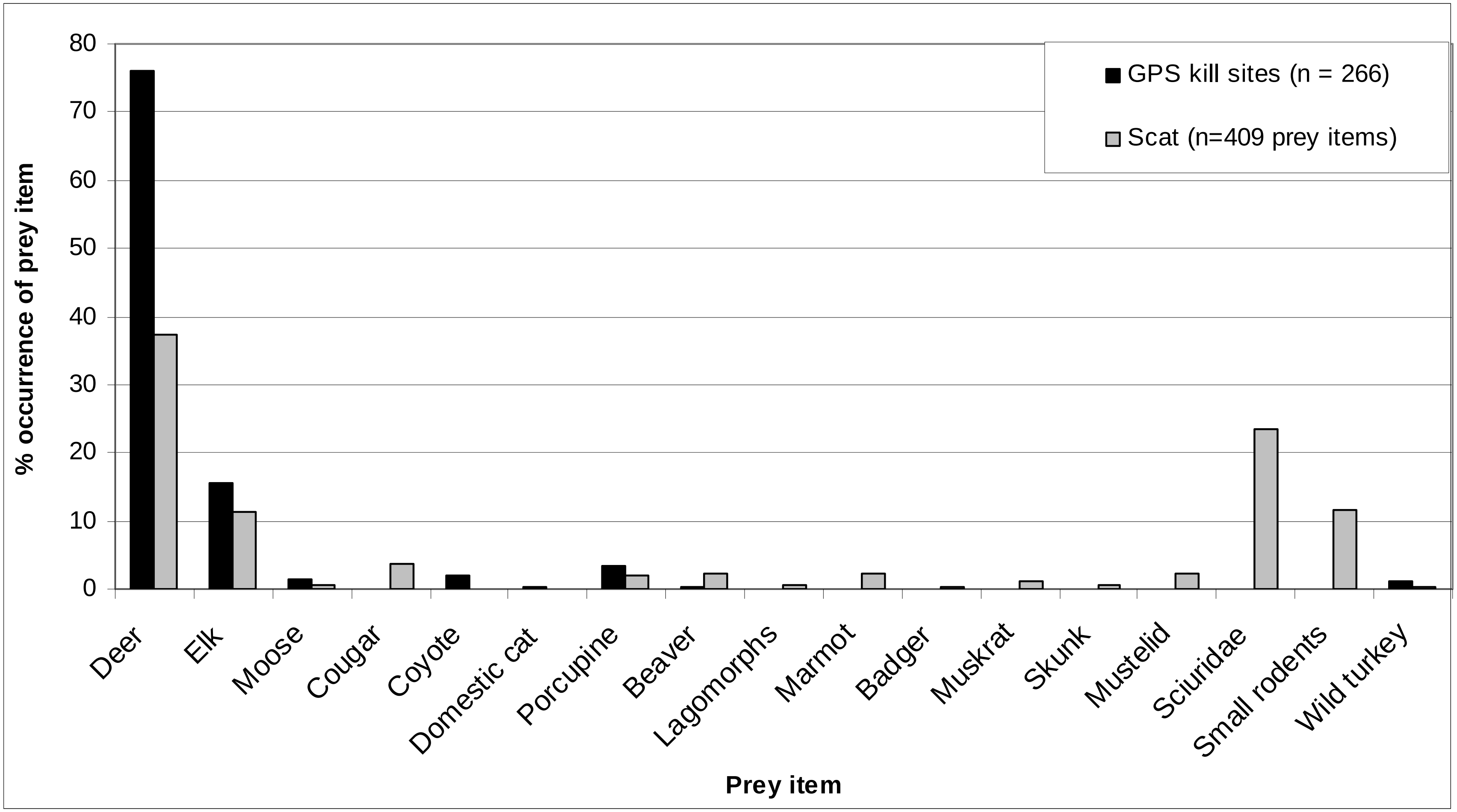

Figure 1. Occurrence of prey items found at kill sites and occurrence of prey items relative to all prey items in scat samples from Cypress Hills Interprovincial Park, May 2008 - December 2009.

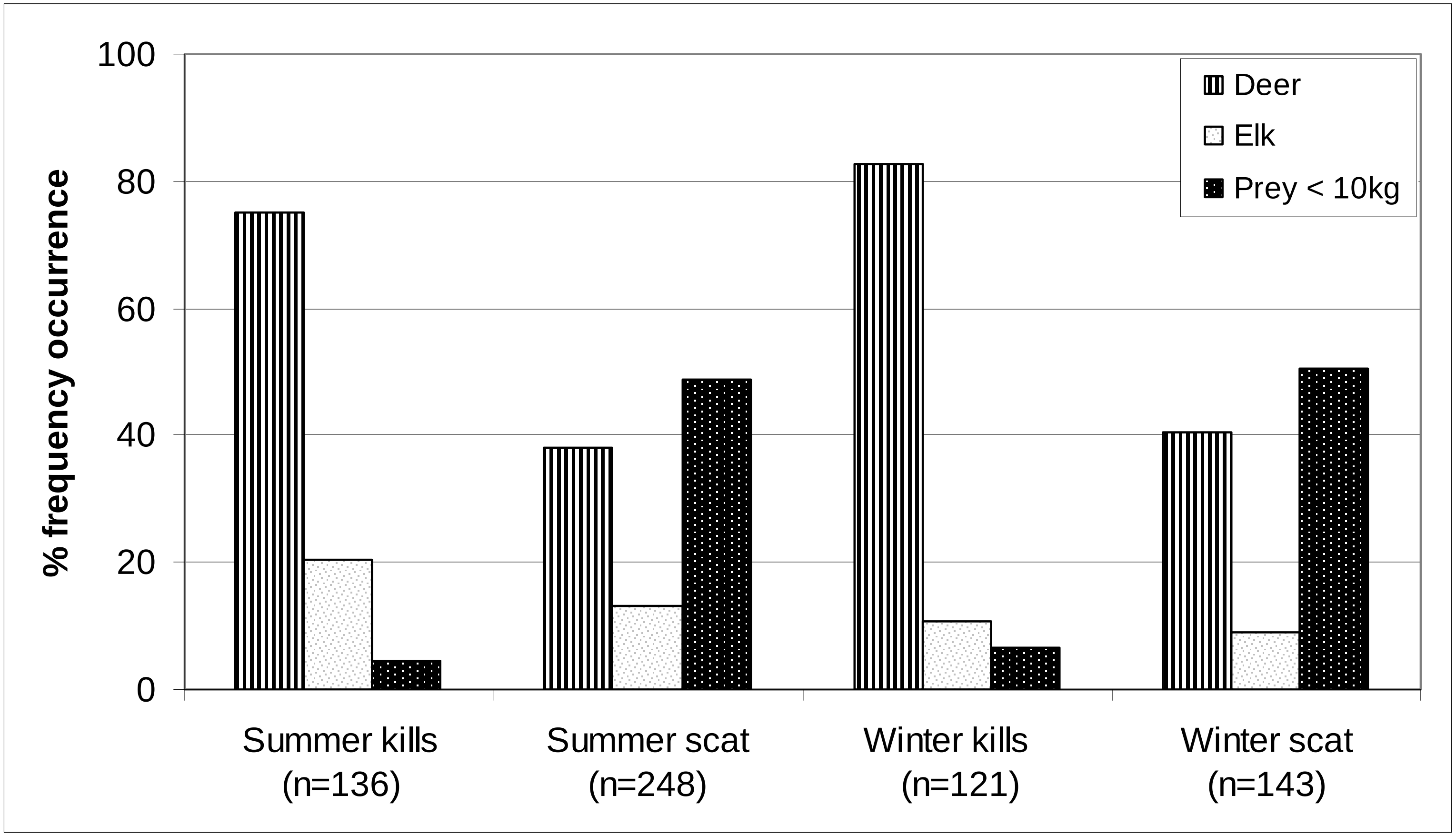

Figure 2. Occurrence of prey items found at kill sites, and occurrence of prey items relative to all prey items in scat samples in summer (May to September) and in winter (October to April), Cypress Hills Interprovincial Park, May 2008-December 2009.

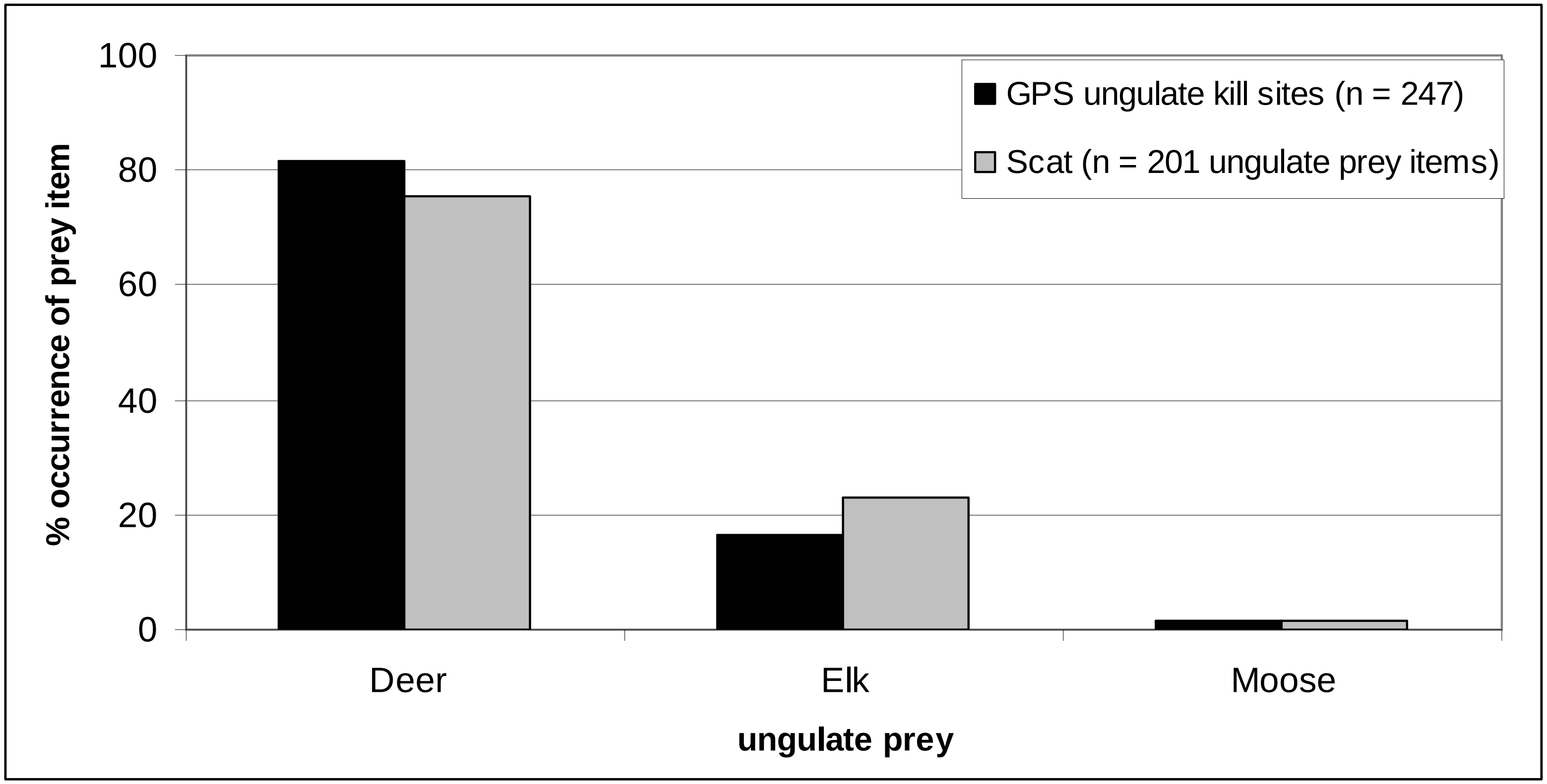

Figure 3. Occurrence of ungulate prey items found at kill sites, and occurrence of deer, elk and moose relative to all ungulate prey items in scat samples, Cypress Hills Interprovincial Park, May 2008-December 2009.

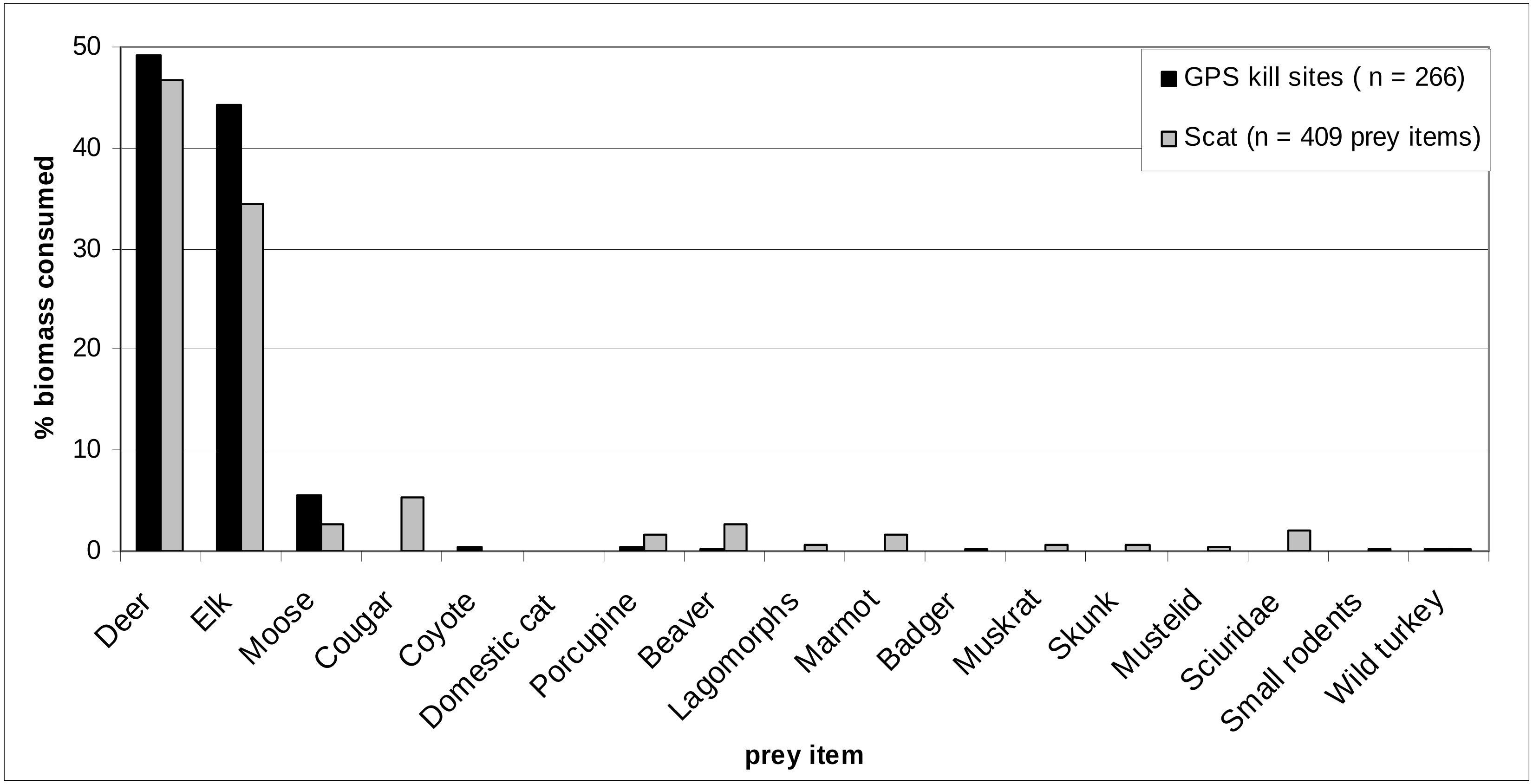

Figure 4. Percent biomass consumed of each prey item at GPS cluster-located kill sites, and from scat analysis (using number of prey items relative to total number of prey items), Cypress Hills Interprovincial Park, May 2008- December 2009.

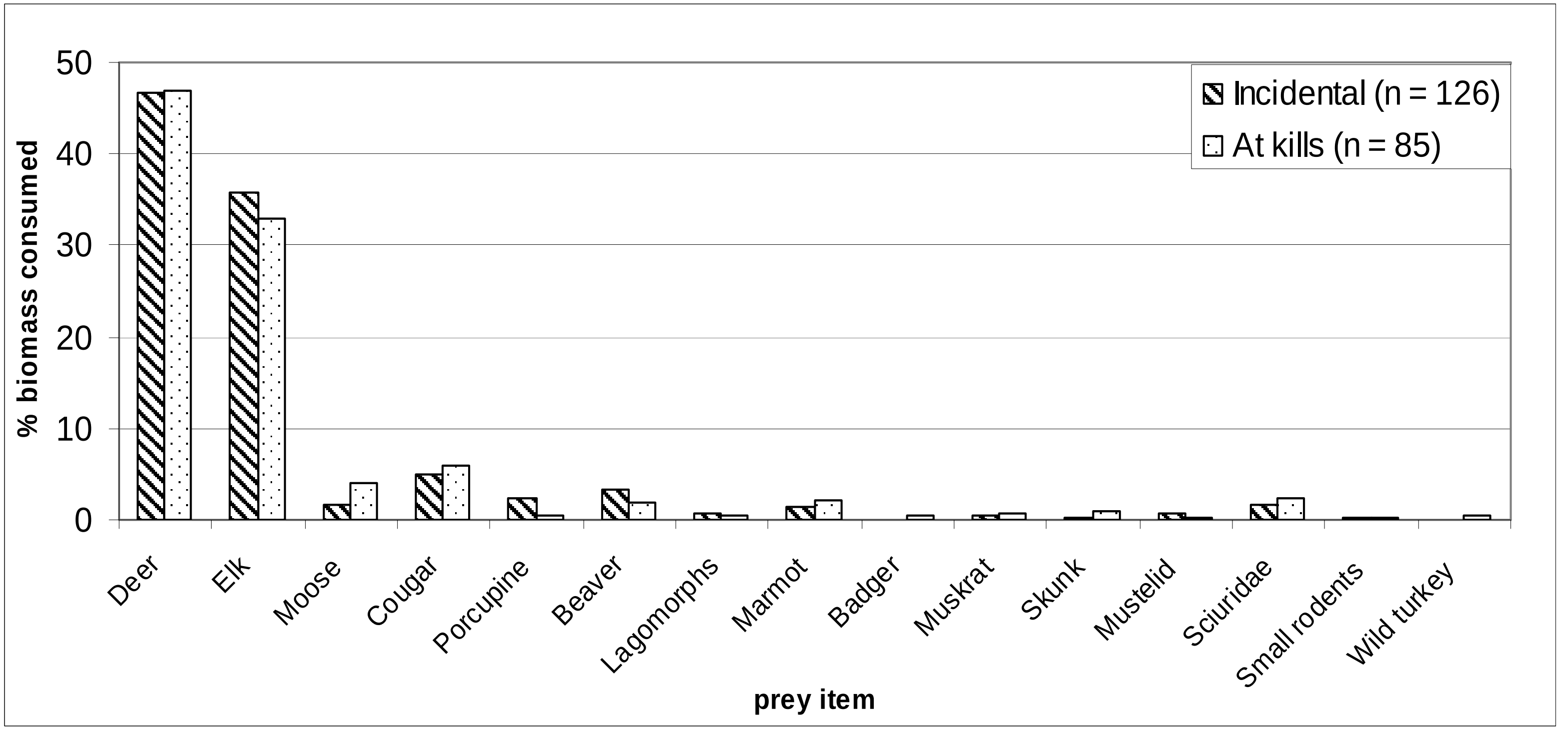

Figure 5. Percent biomass consumed from scat samples collected at kill sites located using GPS cluster techniques and incidentally on trails in Cypress Hills Interprovincial Park, May 2008- December 2009.

Table 1. Composition of cougar diet in Cypress Hills Interprovincial Park, Alberta and Saskatchewan, May 2008-December 2009. Kills located using GPS cluster methods. Scats analyzed by occurrence of prey items relative to total prey items, occurrence of prey items relative to total scats, and occurrence of prey items relative to total hairs.

		Scats				
Prey	**Kills** *n = 266*	**# of prey items** [a] *n = 409*	**Prey items occur** [b] *n = 409*	**Scats occur** [c] *n = 211*	**# of hairs** [d] *n = 4220*	**Hairs occur** [e] *n = 4220*
Deer	202	152	37.2	72.0	2338	55.4
Elk	41	46	11.2	21.8	660	15.6
Moose	4	3	0.7	1.4	34	0.8
Cougar	0	15	3.7	7.1	42	1.0
Coyote	5	0	0.0	0.0	0.0	0.0
Domestic cat	1	0	0.0	0.0	0.0	0.0
Porcupine	9	8	2.0	3.8	122	2.9
Beaver	1	10	2.4	4.7	83	2.0
Lagomorphs	0	3	0.7	1.4	21	0.5
Marmot	0	9	2.2	4.3	44	1.0
Badger	0	1	0.2	0.5	6	0.1
Muskrat	0	5	1.2	2.4	22	0.5
Skunk	0	3	0.7	1.4	17	0.4
Mustelid	0	10	2.4	4.7	122	2.9
Sciuridae	0	96	23.5	45.5	465	11.0
Small rodents	0	47	11.5	22.3	224	5.3
Wild turkey	3	1	0.2	0.5	20	0.5
Total	**266**	**409**	**100**	**193.8**	**4220.0**	**100.0**

[a] 211 scats, containing 409 prey items
[b] % occurrence of prey items relative to total prey items
[c] % occurrence of prey items relative to total number of scats
[d] 211 scats, containing 4220 hairs
[e] % occurrence of prey items relative to total number of hair

Table 2. Calculation of relative biomass consumed by cougars in Cypress Hills Interprovincial Park, Alberta and Saskatchewan, Canada, May 2008 - December 2009. Kill sites located using GPS cluster methods, and scat samples analyzed based on occurrence of prey items relative to all prey items identified.

		Kill sites from GPS clusters (n = 266)			Prey items from scats (n = 409 items)			
Prey	**Est. weight of prey (kg)**[a]	**# of kills**	**Biomass consumed (kg)** [b]	**Biomass consumed as % of all kill sites** [c]	**Prey items occur** [d]	**Correction factor (kg/scat)** [e]	**Total biomass consumed (kg)** [f]	**Relative biomass consumed (kg)** [g]
Deer	40.50	202	8181	49.1	37.2	3.4	126.3	46.7
Elk	180.00	41	7380	44.3	11.2	8.3	93.1	34.5
Moose	227.00	4	908	5.5	0.7	9.9	7.3	2.7
Cougar	57.00	0	0	0.0	3.7	4.0	14.6	5.4
Coyote	16	5	80	0.5	0.0	2.5	0.0	0.0
Domestic cat	4	1	4	0.0	0.0	2.1	0.0	0.0
Porcupine	6.00	9	54	0.3	2.0	2.2	4.3	1.6
Beaver	26.50	1	26.5	0.2	2.4	2.9	7.1	2.6
Lagomorphs	2.73	0	0	0.0	0.7	2.1	1.5	0.6
Marmot	3.40	0	0	0.0	2.2	2.1	4.6	1.7
Badger	7.50	0	0	0.0	0.2	2.2	0.5	0.2
Muskrat	1.20	0	0	0.0	1.2	1.2	1.5	0.5
Skunk	3.05	0	0	0.0	0.7	2.1	1.5	0.6
Mustelid	0.56	0	0	0.0	2.4	0.6	1.4	0.5
Sciuridae	0.23	0	0	0.0	23.5	0.2	5.4	2.0
Small rodents	0.04	0	0	0.0	11.5	0.0	0.5	0.2
Wild turkey	7.40	3	22.2	0.1	0.2	2.2	0.5	0.2
TOTAL		266	16655.7	100	100.0	48.1	270.1	100.0

[a] Lowest estimated live weight (kg) for large mammals, estimated mean live weight (kg) for small mammals, Pattie and Fisher (1999)
[b] estimated weight x # of kills
[c] (estimated weight x # of kills)/total biomass consumed
[d] From Table 1; occurrence of prey items relative to total prey items
[e] from Ackerman et al. (1984) $y = 1.98+ 0.035x$; not for prey <2kg
[f] occurrence of prey items x correction factor
[g] biomass consumed per prey item/total biomass consumed

Table 3. Calculation of relative ungulate biomass consumed by cougars in Cypress Hills Interprovincial Park, May 2008 - December 2009. Kill sites located using GPS cluster methods, and scat samples collected and analyzed based on occurrence of ungulate prey items relative to all ungulate prey items identified.

		Kill sites from GPS clusters (n = 247)			**Ungulate prey from scats (n = 201 items)**				
Prey	**Est. weight of prey (kg) [a]**	**# of kills**	**Biomass consumed (kg) [b]**	**Biomass consumed as % of all kill sites [c]**	**# of prey items [d]**	**Prey items occur [e]**	**Correction factor (kg/scat) [f]**	**Total biomass consumed (kg) [g]**	**Relative biomass consumed (kg) [h]**
Deer	40.5	202	8181	49.7	152	75.6	3.4	256.9	55.7
Elk	180.0	41	7380	44.8	46	22.9	8.3	189.5	41.1
Moose	227.0	4	908	5.5	3	1.5	9.9	14.8	3.2
TOTAL		247	16469	100	201	100	21.6	461.2	100.0

[a] Lowest estimated live weight (kg) for large mammals, Pattie and Fisher (1999)
[b] estimated weight x # of kills
[c] (estimated weight x # of kills)/total biomass consumed
[d] occurrence of prey items relative to all prey items
[e] From Table 1; occurrence of prey items relative to total prey items
[f] from Ackerman et al. (1984) $y = 1.98 + 0.035x$; not for prey <2kg
[g] occurrence of prey items x correction factor
[h] biomass consumed per prey item/total biomass consumed

LITERATURE CITED

Ackerman, B. B., F .G. Lindzey, and T. P. Hemker. 1984. Cougar food habits in Southern Utah. Journal of Wildlife Management 48:147–155.

Alberta Fish and Wildlife Division. 1992. Management plan for cougars in Alberta. Wildlife Management Planning Series No. 5, Edmonton, Alberta.

Anderson Jr., C. R., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. The Journal of Wildlife Management 67:307–316.

Anderson Jr., C. R., F. Lindzey, K. H. Knopff, M. G. Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America. Pages 41–54 *in* M. Hornocker and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, USA.

Bacon, M., K. Knopff, and M. S. Boyce. 2009. Eastward movement of cougars in Canada: an update from Cypress Hills Interprovincial Park. Wild Felid Monitor 2:19.

Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behaviour in puma. Southwestern Naturalist 50:466–471.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401–2414.

Biswas, S., and K. Sankar. 2002. Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. Journal of Zoology 256:411–420.

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

Burdett, C. L., R. A. Moen, G. J. Niemi, and L. D. Mech. 2007. Defining space use and movements of Canada lynx with global positioning system. Journal of Mammalogy 88:457–467.

Carbone, C., A. Teacher, and J. M. Rowcliffe. 2007. The costs of carnivory. PLoS Biology 5:363–368.

Chetkiewicz, C. L., and M. S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46:1036–1047.

Chetkiewicz, C. L., C. Cassady St. Clair, and M .S. Boyce. 2006. Corridors for Conservation: integrating pattern and process. Annual Review of Ecology, Evolution and Systematics 37:317–342.

Doak, D. F., and M. G. Loso. 2003. Effects of grizzly bear digging on alpine plant community structure. Arctic, Antarctic, and Alpine Research 35:421–428.

Edwards, M. A., J. A. Nagy, and A. E. Derocher. 2009. Low site fidelity and home range drift in a wide-ranging, large Arctic omnivore. Animal Behaviour 77:23–28.

Environment Canada. 2009. National Climate Data and Information Archive. http://climate.weatheroffice.ec.gc.ca/climateData/monthlydata_e.html, accessed 17 November 2009.

Floyd, T. J., L. D. Mech, and P. A. Jordan. 1978. Relating wolf scat content to prey consumed. Journal of Wildlife Management 42:528–532.

Foran, D. R., K. R. Crooks, and S. C. Minta. 1997. Species identification from scat: an unambiguous genetic method. Wildlife Society Bulletin 25:835–839.

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

Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41:201–212.

Franke, K. A., T. Caelli, G. Kuzyk, and R. J. Hudson. 2006. Prediction of wolf (*Canis lupus*) kill sites using hidden Markov models. Ecological Modelling 197:237–246.

Fritts, S. H., E. E. Bangs, J. A. Fontaine, M. R. Johnson, M. K. Phillips, E. D. Koch, and J. R. Gunson. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and Central Idaho. Restoration Ecology 5:7–27.

Gau, R. J., Case, R., Penner, D. F. and P. D. McLoughlin. 2002. Feeding patterns of barren ground grizzly bears in the Central Canadian Arctic. Arctic 55:339–344.

Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. Biological Conservation 122:150–171.

Hebblewhite, M., M. Percy, and E. H. Merrill. 2007. Are all Global Positioning System collars created equal? Corrrecting habitat-induced bias using three brands in the central Canadian Rockies. Journal of Wildlife Management 71:2026–2033.

Husseman, J. S., D. L. Murray, G. Power, C. Mack, C. R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101:591–601.

Kellert, S. R., M. Black, C. Reid Rush, and A. J. Bath. 1996. Human culture and large carnivore conservation in North America. Conservation Biology 10:977–990.

Knopff, K. H., A. A. Knopff, and M. S. Boyce. 2010. Scavenging makes cougars susceptible to snaring at wolf bait stations. Journal of Wildlife Management 74:644–653.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating Global Positioning System telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586–597.

Kortello, D. A., Hurd, E. T. and D. L. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. Ecoscience 14:214–222.

Laundré, J. W., and L. Hernández. 2010. What we know about pumas in Latin America. Pages 76–90 *in* M. Hornocker and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, USA.

Litvaitis, J. A. 2000. Investigating food habits of terrestrial vertebrates. Pages 165–190 *in* L. Boitani and T.K. Fuller, editors. Research techniques in animal ecology. Controversies and consequences. Columbia University Press, New York, USA.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: Evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C., USA.

Merrill, S. B., L. G. Adams, M. E. Nelson, and L. D. Mech. 1998. Testing releasable GPS radiocollars on wolves and white-tailed deer. Wildlife Society Bulletin 26:830–835.

Moore, T. D., L. E. Spence, C. E. Dugnolle, and W. G. Hepworth. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Morehouse, A., and M. S. Boyce. 2009. Wolves eat cattle and we pay for the livestock loss. Alberta Outdoorsmen 11(3):10–12.

Murphy, K., and T. K. Ruth. 2010. Diet and prey selection of a perfect predator. Pages 118–137 *in* Cougar ecology and conservation. *Edited by* M. Hornocker and S. Negri, University of Chicago Press, Chicago, USA.

Musiani, M., and P. C. Paquet. 2004. The practices of wolf persecution, protection and restoration in Canada and the United States. BioScience 54:50–60.

Nelson, M. E., L. D. Mech, and P. F. Frame. 2004. Tracking of white-tailed deer migration by Global Positioning System. Journal of Mammalogy 85:505–510.

Newsome, R. D., and R. L. Dix. 1968. The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. American Midland Naturalist 80:118–185.

Pattie, D. and C. Fisher. 1999. Mammals of Alberta. Lone Pine, Edmonton, Alberta, Canada.

Pepin, D., N. Morellet, and M. Goulard. 2009. Seasonal and daily walking activity patterns of free-ranging adult red deer (*Cervus elaphus*) at the individual level. European Journal of Wildlife Research 55:479–486.

Quigley, H., and M. Hornocker. 2010. Cougar population dynamics. Pages 59-75, *in* M. Hornocker and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, USA.

Reed, J. E., W. B. Ballard, P. S. Gipson, B. T. Kelly, P. R. Krausman, M. C. Wallace, and D. B. Wester. 2006. Diets of free-ranging Mexican Gray Wolves in Arizona and New Mexico. Wildlife Society Bulletin 34:1127–1133.

Reynolds, J. C., and N. J. Aebischer.1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. Mammal Review 21:97–122.

Ross, P. I., M. G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. Canadian Journal of Zoology 74:771–775.

Sand, H., B. Zimmerman, P. Wabakken, H. Andren, and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. Wildlife Society Bulletin 33:914–925.

Stewart, K. M., R. T. Bowyer, J. G. Kie, and M. A. Hurley. 2010. Spatial distributions of mule deer and North American elk: resource partitioning in a sage-steppe environment. American Midland Naturalist 163:400–412.

Tomkiewicz, S. M., M. R. Fuller, J. G. Kie, and K. K. Bates. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B 365:2163–2176.

Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:1491–1499.

Valeix, M., A. J. Loveridge, Z. Davidson, H. Madzikanda, H. Fritz, and D. W. Macdonald. 2010. How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. Landscape Ecology 25:337–351.

Van Dijk, J., K. Hauge, A. Landa, R. Andersen, and R. May. 2007. Evaluating scat analysis methods to assess wolverine *Gulo gulo* diet. Wildlife Biology 13(Suppl.2):62–67.

Webb, N. F., M. Hebblewhite, and E. H. Merrill. 2008. Statistical methods for identifying wolf kill sites using Global Positioning System locations. Journal of Wildlife Management 72:798–807.

Weaver, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. Journal of Wildlife Management 57:534–538.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation 3:165–173.

Zimmermann, B., P. Wabakken, J. Sand, H. C. Pedersen, and O. Liberg. 2007. Wolf movement patterns: a key to the estimation of kill rate? Journal of Wildlife Management 33:1177–1182.

CHAPTER 3

FEAR OF LARGE CARNIVORE MOVES WILD UNGULATES OUT OF PARK ONTO AGRICULTURAL LANDS

INTRODUCTION

The relationship between humans and large carnivores is complicated and controversial. Historically, large predators were perceived as competition for food and a risk to the safety of settlers and their livestock (*1*). Predators were heavily hunted, trapped and poisoned, sometimes to the point where species such as the cougar (*Puma concolor*), wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) were extirpated from much of their original range (*2, 3*). Today, large carnivore populations have begun to reclaim portions of their former range, and research has revealed the important role they play in ecosystem dynamics, including top-down effects on prey populations resulting in the restoration of lower trophic levels (*4*).

Despite ecological benefits, the presence of a large carnivore can have negative effects on prey and humans. Cougar predation on bighorn sheep (*Ovis canadensis*) in California led to bighorns being listed as an endangered species by the U.S. Fish and Wildlife Service (*5*). Wolf predation has been documented as a major cause of caribou (*Rangifer tarandus)* mortality, contributing to a global decline to the point of near or full extinction of several herds (*6*). In addition, large carnivores can cause livestock depredation, a concern that resulted in long delays for wolf restoration into the greater Yellowstone region of the United States (7). Despite increasing interest in preserving wildlife, rural communities continue to struggle with livestock loss to predators, and negative human-wildlife encounters are increasing; during the past 20 years the number of cougar attacks on humans is more than double those in the previous hundred (8). These re-established populations of predators have rekindled conflicts with humans, and test our value system as we learn the importance of sustaining dangerous predators that often are keystone species with disproportionate influence on ecosystem structure and function.

Of all carnivores in North America, cougars in particular are achieving an astounding natural re-establishment throughout the western and mid-western states and provinces (*9*). Cougars' extraordinary dispersal capabilities have been documented since the advent of Global Positioning System (GPS) radiocollars; in 2004, a male dispersed 1,067km from South Dakota to Oklahoma (*10*), and in 2005, a female travelled over 1,300km through Utah and Colorado (*11*). The expansion of white-tailed deer (*Odocoileus virginianus*) populations affords cougars an abundant food supply throughout the continent (*12*). However, livestock and agriculture dominate most of central North America, and only in small fragments of forest can cougars avoid conflicts with cattle ranching and persecution by humans long enough to establish resident populations. Although extinction risk might be higher in these small fragments of habitat, they also serve as stepping stone populations facilitating gene flow and expansion to more distant populations (*13*).

My study occurred in Cypress Hills Interprovincial Park, a 400km^2 forested region that rises more than 500 m above the surrounding prairie ecosystem in southeast Alberta and southwest Saskatchewan, Canada (49°40´N, 110°15´W). Cougars and wolves were eradicated from the Cypress Hills nearly 100 years ago, allowing wild ungulate populations to increase to high densities, especially inside the park boundary where there are few sources of mortality. Beginning in the late 1990s, occasional cougar sightings were reported in the Cypress Hills. Sightings continued to increase during the later 2000s, and wildlife cameras provided conclusive evidence of the return of cougars; during my 3-year study from 2007 to 2009, I captured cougars on cameras 73 times, including several family groups (Fig. 1). Using GPS radiocollars, wildlife cameras and snowtracking, I estimated an interprovincial population of 15-20 resident adult cougars in 2009. Combined with the number of kittens identified in winter 2009, I estimated a density of 6.5-8.25 cougars/100 km^2, one of the highest ever reported (*14*).

For ungulates living in a relatively predator-free environment such as the Cypress Hills, a new carnivore creates a landscape of fear where predation success is dependent upon the behavioural changes-or lack thereof-by naïve prey (*15*). Previous research indicates that prey commonly display anti-predator behaviours, but tactics differ by species and can include larger group size, increased vigilance, cryptic or time-specific (i.e., diurnal or nocturnal) movements and feeding patterns, diet selection involving short handling times, and modified escape behaviours (*16*). Many of these behaviours result in a trade-off between locations that have the most desirable food and habitat and locations with least risk of predation (*17*). As early as the first cougar field study in the 1960s, predator impact on deer (*Odocoileus sp.*) and elk (*Cervus elephus*) distribution was apparent, as Hornocker noted: "when a kill is made… deer and elk immediately leave the area, cross to the far side, and in some instances leave to enter a different drainage" (*18*: pp. 35). Elk behaviour and habitat selection in Yellowstone National Park was dramatically altered when wolves were reintroduced, shifting to steeper sloped, forested cover in the summer and grouping up into large herds during winter (*19*).

These striking changes in prey behaviour and distribution documented in previous large carnivore studies motivated me to assess whether the renewed presence of cougars in the Cypress Hills was causing similar habitat shifts by wild ungulates. Cougars have direct effects on prey populations; 76% of kills in the Cypress Hills were deer, and 15% were elk (*20*). To determine whether cougars also have had indirect effects on the prey by altering their behaviour and habitat selection, I examined patterns in ungulate distribution recorded during the past decade.

Cougars' avoidance of open grasslands and agricultural lands has been well documented in habitat-selection studies (*21*), and telemetry data from 6 adult cougars in the Cypress Hills revealed their strong selection for proximity to forest cover; they seldom ventured onto grasslands outside the park, even at night (Fig. 2), and over 70% of their kills occurred in forest cover. Ungulates, though, had been using the park, void of large predators until the return of cougars, to evade human disturbances on the adjacent private lands. Cypress Hills prohibited snowmobiling, ATVs, and deer hunting, and human and road density was low, making an attractive habitat for wildlife, as elk in particular are sensitive to human disturbances (*22*). Hunting activity is much more intense on private land than the limited-quota hunt for elk that occurs inside the park, and because harvest can have strong influence on the abundance of elk (*23*), I expected abundance to remain high inside the park, but with more frequent observations of elk outside the park subsequent to the recovery of the cougar population. Mule deer (*O. hemionus*) select open habitats with rugged terrain, allowing them to detect predators from long distances (*24*). Despite forest cover prevalent in the park, mule deer abundance was high inside the park prior to cougar expansion because deer hunting was prohibited. After the park and forest cover was no longer a safe haven, I expected mule deer abundance to decrease in the park and distribution to shift to the open, non-forested lands more typical of mule deer. White-tailed deer thrive in agricultural edge habitats (*25*) but like mule deer, they had a safe haven inside the park where they could not be hunted. With a predator back in the forests, I expected white-tailed deer distribution to shift out of the security of the park, where the frequency of observations would increase on the agricultural interface of landscapes surrounding the park. In response to the rapidly expanding cougar population inside the park, I tested 3 hypotheses: (i) mule deer distribution shifted out of the forest where predation risk was highest, (ii) white-tailed deer distribution increased in grasslands and agricultural land where cougar presence was lower, and (iii) elk distribution shifted outside the park where the risk of cougar predation was lower.

METHODS

Aerial ungulate surveys

Winter aerial ungulate surveys in the Cypress Hills have been conducted annually since 1977 to manage elk harvests. Because the cougar population increased since the mid-2000s, I analyzed aerial survey data collected each winter from 2000 to 2009. Each year, traditional elk wintering grounds were initially surveyed, followed by detailed aerial coverage of 4 identified survey units which include all forested areas of the park and adjacent lands. Although there are constraints of sightability in forest compared to open land cover types (*26*), I assumed that that bias was the same each year because the observers and survey methods were identical throughout the study period.

Statistical analysis

Using a Geographical Information System (GIS) map of the study area in ArcMap 9.2 (ESRI 2006), I placed all ungulate locations on a 1-km^2 raster grid. I constrained my analysis to known cervid habitats during that decade, defined by the observation of any cervid during aerial surveys in any year between 2000 and 2009. I characterized each grid cell based on the dominant land-cover type, and denoted whether the cell was inside (1) or outside (0) the park boundary. I used zero-inflated negative binomial (ZINB) regression to characterize the distribution of elk and white-tailed deer and the relative abundance of mule deer as functions of the park boundary. In addition, the distribution of mule deer was modelled as a function of the amount of forest cover within each 1-km^2 pixel. Unlike Poisson regression, negative binomial does not assume equal variance and mean but rather that the variance is greater than the mean, which is more appropriate to use in ecological studies because wildlife species such as ungulates are often aggregated into groups (*27*). Zero-inflated methods simultaneously model the probability that the species occupies the grid cell (which gives relative distribution) and the relative abundance of the species (*28*). Predictor covariates for each species were selected *a priori* based on previously published habitat selection models (*29*).

RESULTS

Behavioural responses to the new source of predation risk were strongest in mule deer. Mule deer abundance decreased inside the boundary of the park relative to outside (β = - 0.074, *P* = 0.018), and their distribution shifted out of the forest relative to grasslands and agricultural land cover types (β = 0.133, *P* = 0.001). The proportion of mule deer counted on private land outside the park has increased by 6% per year during the past decade even though total counts of mule deer decreased throughout the study period (β = -0.037, *P* = 0.03). In contrast, white-tailed deer relative abundance increased on both grassland (β = 0.355, *P* = 0.033) and agricultural land (β = 0.44, *P* = 0.008), and their proportional distribution shifted from inside the protected area to outside the park boundary (β = 0.153, *P* = 0.001). Although elk abundance remained higher inside the park (β = 0.86, *P*= 0.019), during the period of increase in cougar abundance a higher proportion of elk occurred outside the park boundary (β = 0.144, *P* = 0.047) (Table 1).

DISCUSSION

The shift in the distribution of cervids demonstrates that cougars have restored a landscape of fear for prey in the Cypress Hills, causing them to leave the security of the protected park and forest cover that now harbours a highly effective predator (Fig. 3). These results are corroborated by local ranchers, who have observed an increase in deer on their agricultural land subsequent to the return of cougars to the Cypress Hills. Conflicts between ranchers and elk have been well documented in this region as well as elsewhere in western states and provinces (*30, 31*); elk forage on and damage crops, and they compete with livestock on rangelands. However, predation has long been recognized as beneficial for redistributing wild ungulates that become so abundant that they alter vegetation (*18*). Decreased grazing pressures inside the park might help to reverse forest encroachment that has occurred in the Cypress Hills during the past 50 years (*32*). In addition, with fewer deer in the forest cougars will either move onto the grassland where prey is abundant-unlikely based on patterns of cougar habitat selection (*21*) -or disperse.

When new predators establish and their population explodes within a decade, as has been the case for cougars in the Cypress Hills, we expect significant changes for the entire ecosystem (*4*). Naïve prey that have lived with little fear of large carnivores for over 100 years must adopt new behaviours, within a single generation, to avoid death. Similarly, naïve humans also must adopt new behaviour as predators expand across the continent to reclaim portions of their former ranges (*33*). Balancing ecological tradeoffs between human and wildlife interests is a challenging issue that wildlife managers throughout North America now face, and must be resolved if there is any hope for coexistence.

Figure 1. Family of three cougars travelling along a hiking trail in Cypress Hills Interprovincial Park-Alberta, December 23 2009. Photo captured on a Reconyx RC55 RapidFire camera (Reconyx, Inc., Holman, WI, USA).

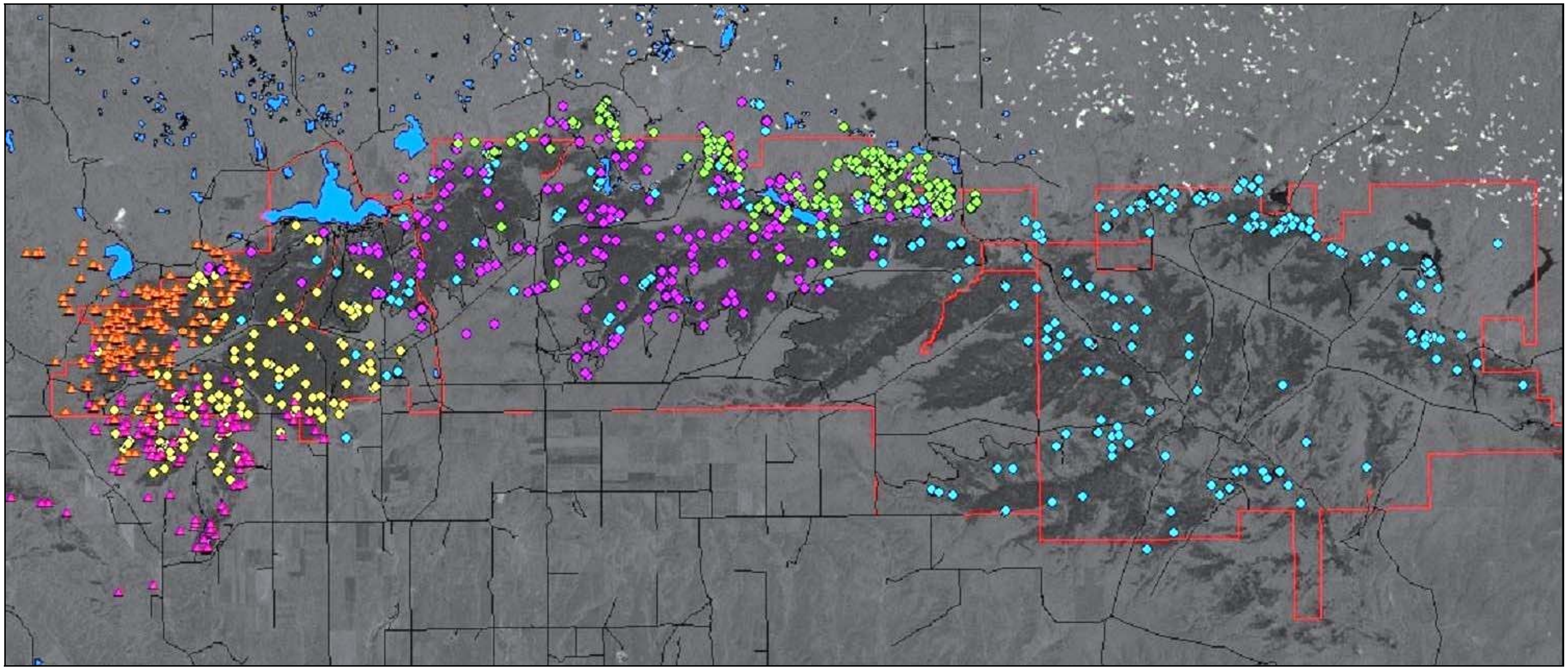

Figure 2. GPS telemetry relocations of six radiocollared cougars (coloured dots) monitored 2008-2009 in Cypress Hills Interprovincial Park, Canada. The red line is the park boundary, and the dark-shaded areas are forest.

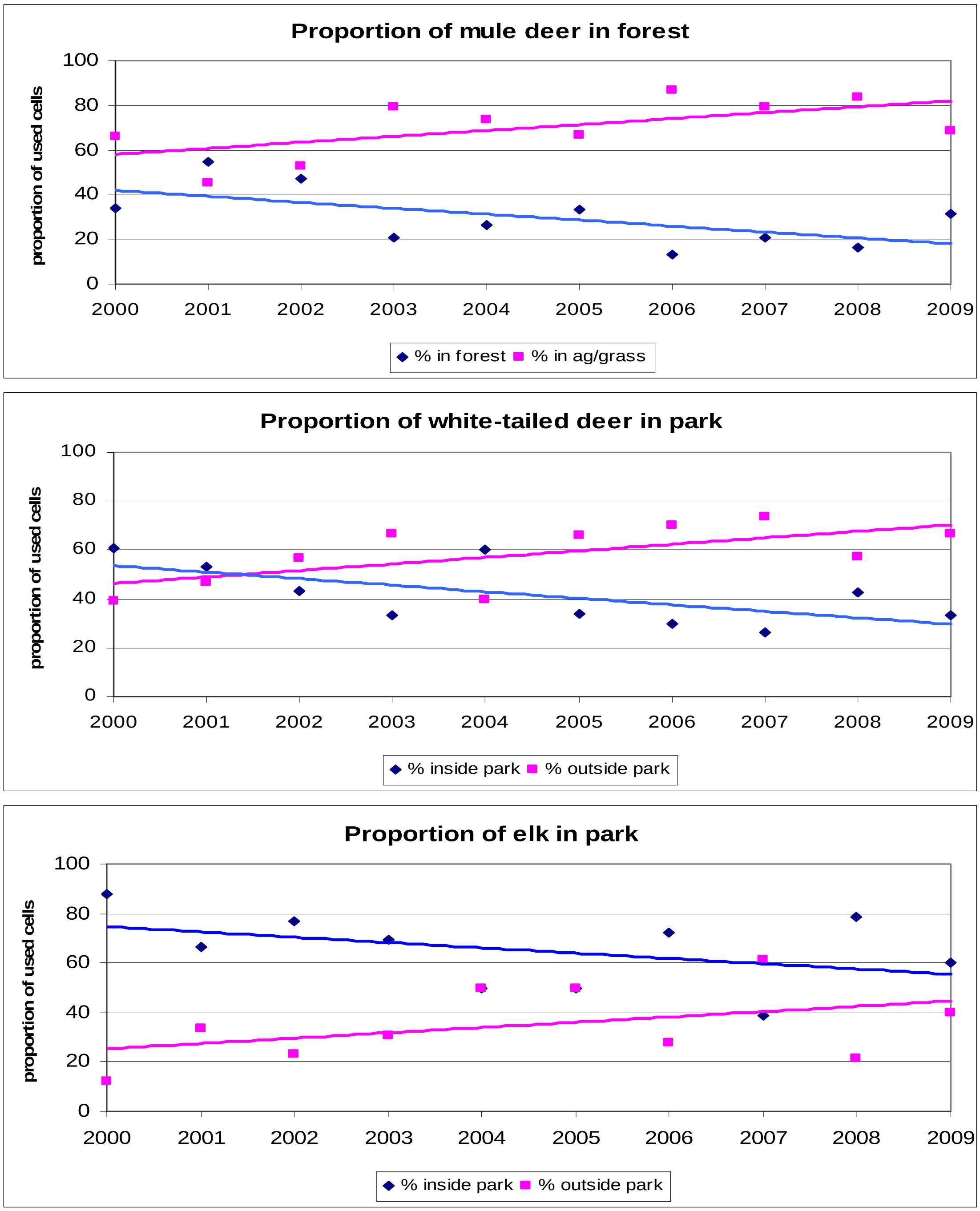

Figure 3. The proportion of mule deer distribution as a function of forest cover and the proportion of elk and white-tailed deer distribution as a function of the park boundary, in Cypress Hills Interprovincial Park, 2000-2009.

Table 1. Estimated coefficients, standard error (SE), p-value and 95% confidence intervals (CI) for zero-inflated negative binomial (ZINB) models used to estimate change in distribution over time for elk, mule deer and white-tailed deer populations in Cypress Hills Interprovincial Park, 2000-2009.

Species	Variable	Coeff.	SE	P value	95% CI	Z-stat for zero-inflation
Elk	park	0.86	0.268	0.019	(0.139, 1.58)	2.29
	year	0.021	0.064	0.739	(-0.104, 0.147)	
	-cons	-40.76	128.37	0.751	(-292.36, 210.84)	
Inflate	park X year	0.144	0.073	0.047	(0.002, 0.287)	
	park	-290.6	145.8	0.046	(-576.37, -4.804)	
	year	0.007	0.054	0.896	(-0.098, 0.113)	
	-cons	-12.42	108.3	0.909	(-224.7, 199.9)	
Mule deer	park X year	-0.074	0.031	0.018	(-0.135, -0.012)	8.12
	year	-0.037	0.017	0.03	(-0.071, -0.0035)	
	park	148.05	62.59	0.018	(25.36, 270.74)	
	-cons	77.46	24.801	0.026	(9.25, 145.67)	
Inflate	forest X year	0.133	0.04	0.001	(0.052, 0.214)	
	forest	-265.6	83.2	0.001	(-428.72, -102.6)	
	year	-0.035	0.021	0.104	(-0.077, 0.007)	
	-cons	71.35	43.2	0.099	(-13.32, 156.03)	
White-tailed deer	grass	0.355	0.166	0.03	(0.027, 0.68)	4.36
	ag	0.44	0.165	0.008	(0.115, 0.764)	
	shrub	0.251	0.189	0.184	(-0.119, 0.621)	
	year	0.026	0.021	0.22	(-0.015, 0.067)	
	-cons	-51.36	42.62	0.228	(-134.9, 32.19)	
Inflate	park X year	0.153	0.046	0.001	(0.062, 0.244)	
	park	-307.15	93.1	0.001	(-489.63, -124.67)	
	year	-0.119	0.03	0.00	(-0.178, -0.06)	
	-cons	241.18	60.85	0.00	(121.9, 360.4)	

REFERENCES AND NOTES

1. S.R. Kellert, M. Black, C. Reid Rush, A.J. Bath, *Conserv. Biol.* **10**, 977– 990 (1996).

2. J. Berger, in *Behavioral Ecology and Conservation Biology,* T. Caro, Ed. (Oxford University Press, USA, 1998), pp. 80–100.

3. J. Terborgh *et al* , in *Continental Conservation,* M.E. Soule, J. Terborgh, Eds. (Island Press, USA, 2000), pp. 39–64.

4. R.L. Beschta, W.J. Ripple, *Biol. Conserv.* **142**, 2401–2414 (2009).

5. C.L. Hayes, E.S. Rubin, M.C. Jorgensen, R.A. Botta, W.M. Boyce, *J.Wildl. Manage.* **64,** 954–959 (2000).

6. L.S. Vors, M.S. Boyce, *Global Change Biol.* **15**, 2626–2633 (2009).

7. S.H. Fritts *et al*, *Restor. Ecol.* **5**, 7–27 (1997).

8. L.L. Sweanor, K.A. Logan, in *Cougar ecology and conservation,* M. Hornocker, S. Negri, Eds. (University of Chicago Press, Chicago, USA, 2010), pp. 190–205.

9. C.R. Anderson Jr., F. Lindzey, K.H. Knopff, M.G. Jalkotzy, M.S. Boyce in *Cougar ecology and conservation,* M. Hornocker, S. Negri, Eds. (University of Chicago Press, Chicago, USA, 2010), pp. 41–54.

10. D.J. Thompson, J.A. Jenks, *J. Wildl. Manage.* **69**, 818–820 (2005).

11. D.C. Stoner, W.R. Rieth, M.L. Wolfe, M.B. Mecham, A. Neville, *J. Wildl. Manage.***72**, 933–939 (2008).

12. S.D. Cote, T.P. Rooney, J-P. Tremblay, C. Dussault, D.M. Waller, *Annu. Rev. Ecol. Evol. Syst.* **35**, 113–147 (2004).

13. L.L. Sweanor, K.A. Logan, M.G. Hornocker, *Conserv. Biol.* **14**, 798–808 (2000).

14. H. Quigley, M. Hornocker, in *Cougar ecology and conservation,* M. Hornocker, S. Negri, Eds. (University of Chicago Press, Chicago, USA, 2010), pp. 59–75.

15. J.S. Brown, J.W. Laundré, M. Gurung, *J. Mammal.* **80**, 385–399 (1999).

16. S.L. Lima, L.M. Dill, *Can. J. Zool.* **68,** 619–640 (1990).

17. S.L. Lima, *Bioscience* **48**, 25–34 (1998).

18. M.G. Hornocker, *Wildl. Monogr.* **21**, 3–39 (1970).

19. J.S. Mao *et al*, *J. Wild. Manage.* **69**, 1691–1707 (2005).

20. See Chapter 2.

21. B.G. Dickson, P. Beier, *J. Wild. Manage*. **66**, 1235–1245 (2002).

22. L. M. Naylor, M. J. Wisdom, R. G. Anthony, *J. Wild. Manage*. **73**, 328–338 (2009).

23. J. A. Vucetich, D. W. Smith, D. R. Stahler, *Oikos* **111**, 259–270 (2005).

24. S. Lingle, W.F. Wilson, *Ethology* **107**, 125–147 (2001).

25. S. J. Williamson, D. H. Hirth, *Wildl. Soc. B*. **13**, 252–257 (1985).

26. P.J.S. Fleming, J.P. Tracey, *Wildlife Res.* **35**, 258–267 (2008).

27. T.R.E. Southwood, P.A. Henderson, *Ecological Methods* Third Edition (Blackwell Science, Oxford U.K., 2000).

28. S.J. Wenger, M.C. Freeman, *Ecology* **89**, 2953–2959 (2008).

29. The land cover of the 270 used cells were comprised of 42% forest, 32% grasslands, 14% agricultural lands, 11% shrub, and 1% water. The zero-inflated model accounts for an excess of zeros, or "unused", cells in each year of the analysis, verified by a Vuong (V) test. We selected predictor covariates based on habitat studies previously listed (*22-25)*. All analyses were conducted in STATA 11.0 (STATA 2009).

30. T.M. Hegel, C.C. Gates, D. Eslinger, *J. Environ. Manage.* **90**, 222–235 (2009).

31. J.R. Lacey, K. Jamtgaard, L. Riggle, T. Hayes, *J. Range Manage.* **46,** 31–37 (1993).

32. K.J. Widenmaier, W.L. Strong, *For. Ecol. Manage.* **259,** 1870–1879 (2010).

33. J.A. Shivik, *Bioscience* **56**, 253–259 (2006).

CHAPTER 4

GENERAL CONCLUSIONS AND COUGAR MANAGEMENT RECOMMENDATIONS

Recovery of cougars (*Puma concolor*) in North America is a wildlife success story, making a remarkable comeback during the past few decades by first rebounding in the West and then naturally dispersing eastward. Their numbers have increased in the Midwest to the point that several states have reclassified cougars as furbearers or big game animals (Anderson et al. 2010), and confirmed sightings, tracks, scat and carcasses in eastern provinces and states signal an increasing presence there also (Harris 2007; Absher 2009). On the cusp of their movement to the east, my research in southeast Alberta and southwest Saskatchewan provided a unique opportunity to study the ecological aspects of a re-established population, as well as address the human concerns that are common in any area where a predator re-populates.

At the completion of my 3-year study, data from radiocollars, wildlife cameras and snowtracking has helped me to identify 15 to 20 adult cougars and at least that many kittens/juveniles in Cypress Hills Interprovincial Park. In this isolated patch of habitat, the cougar population exploded within a decade to a density of 6.5-8.25 cougars/100km^2. Based on photos from wildlife cameras as well as data from our radiocollared cats, I believe that 3 - 4 of these cougars are adult males, which means they have either reduced their typical home ranges, which can encompass areas larger than 750km^2, or are overlapping extensively (Logan and Sweanor 2010). The home ranges of 3 radiocollared females overlapped nearly 100%, and we identified at least 2 other adult females in that same territory during attempted captures in winter 2009 (Figure 1). This high proportion of home range overlap is rarely reported in scientific literature but may become more common as cougars re-establish in small patches of suitable habitat amidst the open prairies of central North America (Logan and Sweanor 2010).

Cypress Hills is likely a source population of cougars, where productivity exceeds mortality (Pulliam 1988). Sweanor et al. (2000) suggested that populations in protected areas serve as "robust, biological savings accounts that contribute to population resistance" (806). The Cypress Hills likely serves as a jumping-off point for further expansion eastward to other small patches of forest in the prairies such as Moose Mountain Provincial Park in southwest Saskatchewan, and Duck Mountain Provincial Park and Riding Mountain National Park in Manitoba. These stepping stones of preferred cougar habitat could eventually lead to the expansive forests of Northern Ontario. Although the estimated size of the population would likely support the removal of a few cougars by hunting each year, the Cypress Hills may be better managed as a source population (i.e. closed to hunting) assuming cougar expansion is desired by interest groups (Laundré and Clark 2003).

Although there are no wolves (*Canis lupus*) or bears (*Ursus sp*.) as possible predators of cougars, there are other sources of mortality in the Cypress Hills. Between 2004 and 2009, 12 cougars were reported shot or snared incidentally outside the park boundary (D. Etherington, Alberta Sustainable Resource Development, personal communication; J. Stock, Saskatchewan

Environment, personal communication). In addition, it is not uncommon for cougars to be injured or killed by prey (Hornocker 1970; Ross et al. 1995; Logan and Sweanor 2001, 137). Cougar 10118R, an 82kg male captured in 2008, was found dead in an open field frequented by an elk herd, and a necropsy showed his ribs had been crushed which then punctured his lungs; most likely he was kicked by an elk during an attempted predation event.

The high density of cougars also likely results in intraspecific strife. Two specific incidents illustrate this point. First, we analyzed a scat sample from a radiocollared male that was made up entirely of cougar hair (Chapter 2). Although it was common to find cougar hair in scat as a result of grooming, this sample was distinct because it had no other hair types and indicated that he had likely killed another cougar. Male infanticide is commonly responsible for a significant number of kitten deaths (Logan and Sweanor 2001, 120), and the Cypress Hills cougars would be no exception. Second, we encountered an incident where kittens either dispersed at an unusually young age or were killed. Female 10117R had a litter of 4 kittens in July 2008, and we snowtracked the family in February 2009 when at least 3 kittens were alive. Yet this same female had a new den in June 2009, just 4 months after we tracked her family. Based on a 90-day gestational period, the original litter must have been killed, or else they dispersed at 9 months of age, the latter being unlikely based on the typical age of dispersal being between 1 and 2 years (Logan and Sweanor 2010). Intraspecies strife and infanticide by males is likely more common in populations where there is no hunting, such as the Cypress Hills (Cunningham et al. 2001; Logan and Sweanor 2001, 139).

Despite the density of cougars, I found no evidence of livestock depredation in over 300 kill sites and 250 scat samples (Chapter 2). Cattle graze inside the park during the summer and on adjacent land year-round and are thus easily available prey items. However, cougars preferred wild ungulates; deer (*Odocoileus sp.)* accounted for 76% of prey items at GPS clusters and nearly 50% of biomass from scat samples. This is similar to most cougar studies in North America where their primary prey are ungulate species (Murphy and Ruth 2010). Cougars in the Cypress Hills were preying on white-tailed deer (*O. virginianus*) at a higher frequency than mule deer (*O. hemionus*) (59% and 26% of deer kills, respectively). White-tailed deer also increased in abundance during the study period, and that increased availability may explain this selection. Both white-tailed deer and mule deer altered their distribution during the past decade of cougar re-establishment, shifting from inside the forests of the protected park to outside the park boundary onto private agricultural lands and grasslands (Chapter 3). Elk (*Cervus elaphus*) distribution also showed similar movement out of the forests, the preferred habitat type for the cougars. Anti-predator behaviours such as altered distributions are common in most wildlife species (Lima and Dill 1990); the ungulates in Cypress Hills would have had to evolve quickly to avoid death in the forest by the rapidly expanding cougar population.

Cougars are avoiding areas in the park that have a high human presence. Although 4 of the 6 radiocollared cougars had home ranges that included campgrounds in the park townsite, they rarely used those areas during the busy summer season when tourist activity peaked. Sightings during the past 5 years on wildlife cameras and by people in the townsite were significantly lower in the tourist season than in fall and winter when human presence abated. This pattern of avoidance has been documented in other research as well (Sweanor et al. 2008), and should help alleviate some concerns about public safety. The number of sightings of cougars in the townsite also decreased since 2 new park regulations came into effect: first, that cottagers were prohibited from maintaining bird feeders, and second, that cottagers were encouraged to cover in their low decks. These 2 changes have resulted in decreased cougar attractants-deer, birds, and cache spots-in high human use areas, and have successfully deterred cougar presence.

With a dense adult cougar population, it is likely that most or all juveniles will need to disperse from the Cypress Hills region and this could be a potential source of conflict with livestock and humans as young dispersers approach ranches in search of easy prey (Ruth and Murphy 2010). Based on this knowledge, I recommend ongoing research in the Cypress Hills, focused on capturing juvenile cougars and fitting them with ARGOS-GPS radiocollars (Lotek Engineering, Newmarket, ON, Canada). These collars provide researchers with data which can be used to develop models predicting cougar movement across the prairie. Once key habitat features and corridors are identified, they can be managed to allow for continued cougar dispersal in those areas, as well as allowing for precautionary measures to be taken to avoid livestock depredation and other conflicts with humans (Chetkiewicz et al. 2006; Chetkiewicz and Boyce 2009). This will be essential information for wildlife managers as cougars disperse from western populations across the prairies and further eastward.

In addition to continued research, areas with re-establishing cougar populations need to develop a consistent, detailed reporting system. This will help ensure that all signs and sightings that are reported to fish and wildlife officers are reliable, and will produce a database of knowledge accessible to biologists, conservation officers and wildlife managers who have limited experience in identifying cougar signs. A consistent reporting system will also help to create reliable population size and density estimates to ensure management actions in each region, and across the entire province or state, are suitable.

The importance of public outreach and education should not be overlooked when managing a new predator on the landscape (Kellert et al. 1996). Rumours about cougar sightings and attacks result in fear, misconceptions and intolerance. Wildlife managers need to initiate public workshops to share information about cougar biology and management regulations (Cougar Management Guidelines Working Group 2005, 95; Hamilton 2006). Wildlife managers cannot shy away from the challenging questions about human safety and livestock depredation; by doing so, they would alienate their community and increase the spread of misinformation. In the Cypress Hills, rumours spread about how cougars returned to the area, including urban legends that these particular cougars were known problem cases relocated by the government from other western populations. I initiated a public outreach campaign to help educate landowners and tourists about cougar biology, safety precautions and research progress to try to reduce the misconceptions being spread. A proactive approach to effective communication between wildlife professionals and the rural communities they manage will boost tolerance of cougars and reduce negative human-wildlife encounters (Mangel et al. 1996; Messmer et al. 2001).

Cougar are re-establishing viable populations in the fragmented landscape of the prairies, but their survival depends on the landowners that live around these patches of suitable habitat. Governments need to create, and regularly update, management and contingency plans so that there is a pre-determined set of actions when conflicts between cougars and humans occur (Cougar Management Working Guidelines 2005, 101). Local wildlife managers need access to an information database that will assist them in confirming signs and sightings and help them to manage public complaints appropriately. Public education, scientific research, consistent monitoring, a pre-determined management action plan for problem cougars, and a rigorous inter-provincial and cross-border reporting system will all help to mitigate concerns and increase knowledge as cougars continue their eastward migration.

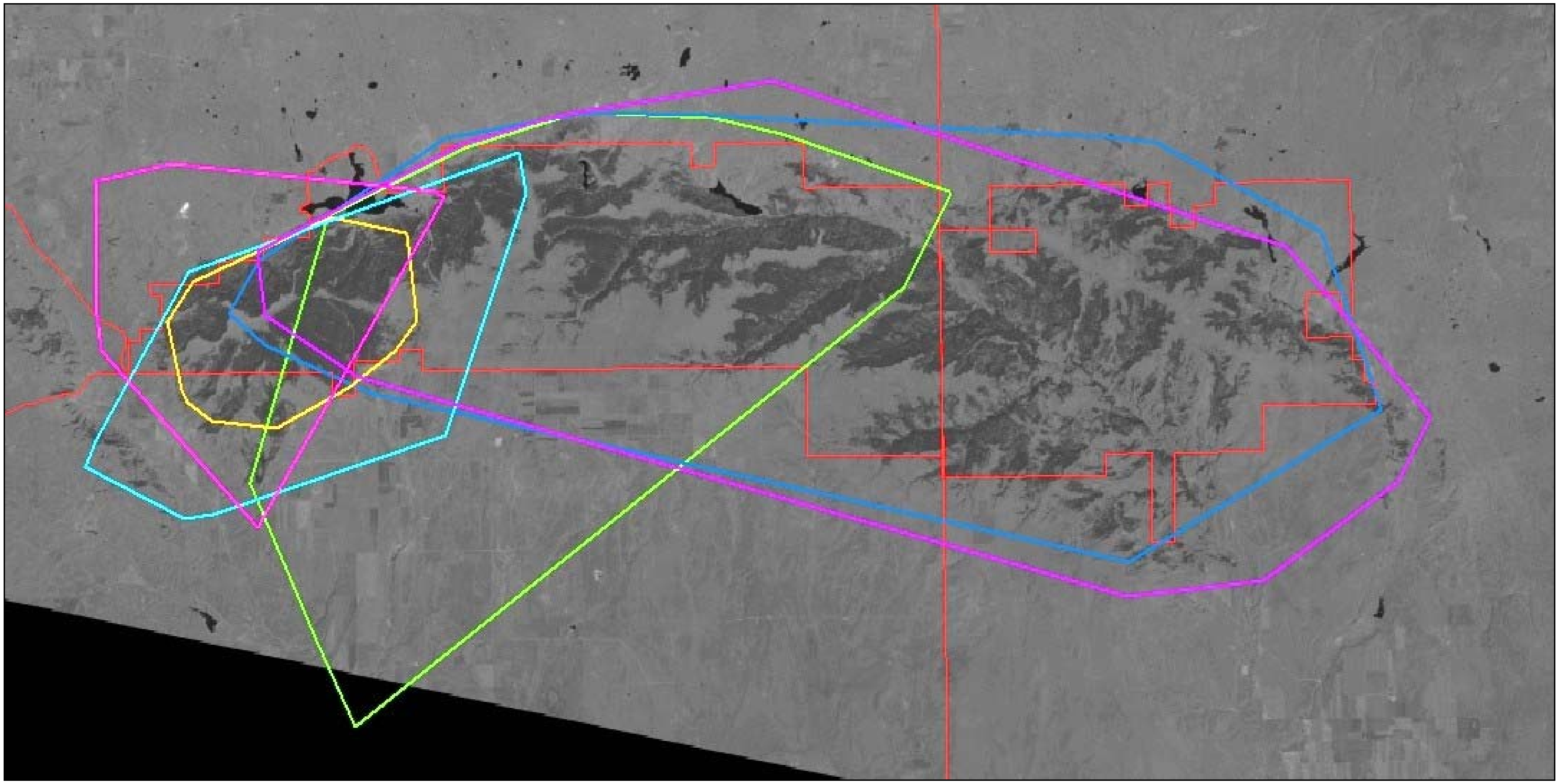

Figure 1. Home ranges of 6 radicollared cougars (coloured polygons), monitored April 2008 - December 2009 in Cypress Hills Interprovincial Park, Canada. The red line is the park boundary.

LITERATURE CITED

Absher, J. R. 2009. Coming to an area near you. Outdoor Life March 2009:31–33.

Anderson Jr., C. R., F. Lindzey, K. H. Knopff, M. G. Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America. Pages 41–54, *in* M. Hornocker and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, USA.

Chetkiewicz, C. L., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for conservation: structure versus function. Annual Review of Ecology, Evolution and Systematics 37:317–42.

Chetkiewicz, C. L., and M. S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46:1036–1047.

Cougar Management Guidelines Working Group. 2005. Cougar Management Guidelines, First edition. WildFutures, Bainbridge Island, Washington, USA.

Cunningham, S. C., W. B. Ballard, and H. A. Whitlaw. 2001. Age structure, survival, and mortality of mountain lions in southeastern Arizona. Southwestern Naturalist 46:76–80.

Hamilton, D. 2006. Cougar hysteria: addressing mountain lion mania in the Midwest and the East. Wild Cat News 2(3):1–7.

Harris, E. 2007. Cougar on the move. Canadian Geographic 127(6):46–47.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:3–39.

Kellert, S. R., M. Black, C. Reid Rush, and A. J. Bath. 1996. Human culture and large carnivore conservation in North America. Conservation Biology 10:977−990.

Laundré, J., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. Animal Conservation 6:159–170.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Logan, K., and L. L. Sweanor. 2010. Behaviour and social organization of a solitary carnivore. Pages 105–117 *in* Cougar ecology and conservation. *Edited by* M. Hornocker and S. Negri, University of Chicago Press, Chicago, USA.

Logan, K. A., and L. L. Sweanor. 2001. Desert Puma: evolutionary ecology and conservation of an enduring carnivore. Washington D.C.: Island Press.

Mangel, M., et al. 1996. Principles for the conservation of wild living resources. Ecological Applications 6:338–362.

Messmer, T. A., D. Reiter, and B. C. West. 2001. Enhancing wildlife sciences' linkage to public policy: lessons from the predator-control pendulum. Wildlife Society Bulletin 29:1253–1259.

Murphy, K., and T. K. Ruth. 2010. Diet and prey selection of a perfect predator. Pages 118–137 *in* Cougar ecology and conservation. *Edited by* M. Hornocker and S. Negri, University of Chicago Press, Chicago, USA.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Ross, P. I., M. G. Jalkotzy, and P.-Y. Daoust. 1995. Fatal trauma sustained by cougars, *Felis concolor*, while attacking prey in southern Alberta. Canadian Field Naturalist 109(3):261–263.

Ruth, T.K., and K. Murphy. 2010. Cougar-prey relationships. Pages 138–172 *in* Cougar ecology and conservation. *Edited by* M. Hornocker and S. Negri, University of Chicago Press, Chicago, USA.

Sweanor, L. L., K. A. Logan, J. W. Bauer, B. Millsap, and W. M. Boyce. 2008. Puma and human spatial and temporal use of a popular California state park. Journal of Wildlife Management 72:1076–1084.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.

APPENDIX A

FREE FELINE FEAST: COUGAR SCAVENGING DOCUMENTED ON WILDLIFE CAMERA

Scavenging by cougars (*Puma concolor*) was rarely reported in early literature about cougar biology, and most long-term studies suggested cougars preferred to kill their own prey; Ross and Jalkotzy (1996) found only 4 incidents of scavenging on moose (*Alces alces*) carcasses during their 13-year study in southwest Alberta, and Logan and Sweanor reported only 16 cases of scavenging in their 10-year study in New Mexico (2001). However, a few incidents of individual cougars scavenging were reported, including a single adult female scavenging on 4 different carcasses during a 22-day period in northeast Oregon (Nowak et al 2000). Lately, reports of cougar scavenging are becoming more common. Bauer et al. (2005) reported 43.5% of carcasses they placed out as bait in California were scavenged by 8 to 12 different cougars, implying that cougars are opportunistic scavengers. Knopff et al. (2010) report that cougars' tendency to scavenge in west-central Alberta is high, making them vulnerable to baited snares along traplines set up for wolves (*Canis lupus*) or coyotes (*Canis latrans*); incidental snaring was responsible for 11% of cougar mortalities during their 4-year study and included healthy adults that were capable of killing live prey.

Even with the advent of Global Positioning Systems (GPS) radiocollars and cluster techniques to locate kill sites (Anderson and Lindzey 2003, Knopff et al. 2009), cougar scavenging events and rates are difficult to quantify. Previous studies have shown cougars will treat scavenged carcasses similar to their own kills, and will cache and cover them with vegetation and dirt. A carcass may be scavenged by numerous species, including coyotes, birds and small mammals, before the researcher can visit it, making it a challenge to determine with confidence whether the cougar was the initial predator. Scavenging that is confused with kills can inadvertently inflate estimated kill rates (Bauer et al. 2005, Knopff et al. 2010).

Motion-activated remote cameras allow researchers to observe wildlife behaviours without capture and immobilization, and can provide a wide variety of information about biological systems including biodiversity (Stein et al. 2008), population sizes, densities and demographics (Jacobson et al. 1997, Karanth and Nichols 1998), the presence of cryptic or rare species (Moruzzi et al. 2002), nest predation (Coates et al. 2008), predation risk in microhabitats (Hernández et al. 2005), and daily wildlife activity patterns (George and Crooks 2006). Although previously limited to film cameras placed in protective boxes, new digital cameras are available with features that include colour photos, infrared flashes, various settings for number of photos per event and time between events, date, time and temperature stamps, and video settings. This non-invasive, relatively inexpensive method of monitoring is becoming more common in wildlife researchers' and managers' toolboxes (Cutler and Swann 1999). Consequently, I was able to use wildlife cameras to observe scavenging by at least 3 different cougars, and visitation by 3 others, on an elk carcass from January to April 2009 in southeast Alberta.

I was notified by a landowner of cougar tracks and scat around an elk (*Cervus elephus*) carcass on 6 January 2009. The elk was approximately 350m south of the boundary for Cypress Hills Interprovincial Park, a protected region in southeastern Alberta and southwestern Saskatchewan (49°40′N, 110°15′W) that has recently seen a natural re-establishment of a dense cougar population (Bacon and Boyce 2009). I visited the elk carcass with the landowner and Alberta Fish and Wildlife officers the following day, and confirmed that it had died from a bullet wound. The landowner had hunters on his property in late November 2008 and it was likely them who had shot but not retrieved the bull elk. The carcass was frozen and had holes in the rump, stomach and back. It did not exhibit the typical signs of a cougar kill (consuming organs first, caching the carcass and covering it with vegetation and hair piles) and we concluded it had been scavenged by coyotes and birds already. There were no fresh cougar tracks.

I set up a Reconyx RC55 RapidFire camera (Reconyx, Inc., Holman, WI, USA) on a tree facing the carcass, approximately 1m off the ground. The landowner also set up his own camera (Stealth Cam, LLC, Grand Prairie, TX, USA) on a game trail leading away from the carcass, and left it up for the month of January. I initially programmed our camera to take 5 pictures per motion, with 5 seconds between photos and 30 seconds between events. The camera took 3,845 photos between 7 January and 13 January before the memory card filled. I checked the camera on 30 January and reprogrammed it to take fewer pictures per event. The memory card once again filled up quickly, largely due to the activities of magpies (*Pica pica*) on the carcass. I checked the camera on 12 March and reset it to take 3 pictures per motion, with 10 seconds between photos. The camera took 3,734 photos before filling up the memory card on 3 April. I removed the camera on 17 April 2009.

I was surprised to identify 6 individual cougars visiting the elk carcass during the 3.5 months that our camera was set up. Many cougars in our study area had lost the tips of the ears or the black tips of their tails, likely from frostbite. These traits, along with body size and the presence or absence of a radiocollar, allowed me to identify many individual cougars despite their single-colour pelage. Cougar 1 (Figure 1) was the most frequent visitor to the elk and spent the most time scavenging on the carcass. She had very short ears, a full tail and no radiocollar, and her body size and configuration indicated she was a female. Cougar 1 was first captured on the camera in the early hours of 8 January-less than 12 hours after I had set up the camera-and spent much of the following 6 days eating, grooming and sleeping next to the elk. She scavenged at all times of the day, and several series of photos show her covering the carcass with dirt and vegetation prior to leaving. She last appeared on camera on 13 January, but may have visited later in the month after the camera's memory card had filled.

Cougar 2 (Figure 2) appeared in early January while Cougar 1 was still feeding off the carcass. Cougar 2 was never at the elk carcass at the same time as Cougar 1. This cougar appeared smaller and younger and had no radiocollar, but very large ears and a full tail. Cougar 2 was never observed consuming meat from the carcass; each of the 4 times it appeared between 11 January and 13

January, the cougar sniffed the elk, walked around the carcass and then left. This juvenile cougar may not have eaten anything from the elk if Cougar 1, an adult, was still using and marking the carcass. Cougar 2 was captured on the landowners' camera on the trail leading away from the carcass on 14 January, the day after our camera ran out of memory, so it might have visited and scavenged on the elk on other occasions that month.

Cougar 3 (Figure 3) was captured on the landowners' camera on 26 January after our camera had run out of memory. This cougar had full ears, a short tail and possibly a radiocollar- we believe it was one of our radiocollared adult females (10117R). After looking at her GPS data from that day, I confirmed that individual had been in that area but not long enough to conclude with certainty that she had been scavenging on the elk. A fourth cougar- another radiocollared female (9977R)- visited and scavenged on the elk carcass in March. Cougar 4 (Figure 4) - easily identified based on a very short tail and ears- arrived at the elk on 19 March at 8:15pm and scavenged for about half an hour before leaving. She returned 11 days later but did not eat.

Cougar 5 (Figure 5) appeared on 23 March and ate a few bites off the carcass. This cougar had a significantly larger body and head size than any other cougar captured on this camera, and it confirmed the presence of an additional male using this small region of suitable habitat. Up until this point, I had considered the possibility that the large, 82 kg male I had radiocollared in 2008 (Bacon and Boyce 2008) was the only male in the Cypress Hills, since the region is only approximately 400km^2 and territorial males can have home ranges more than 700km^2 (Logan and Sweanor 2010). These photographs confirmed that not only females had overlapping home ranges, but so did males.

The last cougar to make an appearance at the nearly depleted elk carcass was a radiocollared female (10118R) with full ears and a full tail (Figure 6). This was a young female and I would later find other incidents of scavenging on elk and moose by her as well (M. Bacon, unpublished data). Cougar 6 first arrived at the elk on 2 April and ate throughout that day and the next, despite the fact that little meat remained on the carcass. She left the carcass frequently and covered it up in between scavenging events. The camera's memory card filled on 3 April, but GPS data from her radiocollar showed that she remained at the carcass consistently until the morning of 8 April. She returned to the elk repeatedly during the week of 21 to 28 April, staying there for most of the nights of 23, 24, and 25 April.

My use of motion-activated cameras confirmed scavenging activity as well as carcass-sharing by cougars. It is unlikely that this was a unique event I happened to catch on camera; cougars may be jumping intraspecific competitors off fresh and scavenged kills frequently, which could inflate estimated predation rates. All 6 cougars that visited and/or scavenged on the elk carcass appeared to be in healthy condition, and I know the 3 with radiocollars were all capable of killing their own prey because I had located kill sites using GPS cluster techniques (Chapter 2). Cougar 6 had other incidents of scavenging and I suspected she was a sub-adult when I captured her in March 2009. Cougar 2 also appeared to be much younger than the others and might have even been a dependent juvenile temporarily separated from its mother.

My use of cameras not only provided evidence of scavenging, but also helped to estimate population size and density for this region. When I started this project in 2007, the population estimate for this 400km^2 park was between 5 and 10 adults. By the end of my study, that estimate had doubled, thanks in part to my use of wildlife cameras on game and hiking trails throughout the park, and with my identification system judging ear and tail characteristics, body size, presence of radiocollars, and size of family groups. When combined with the number of kittens identified during winter 2009, I estimated cougar density of 6.5-8.25 cougars/100 km^2, one of the highest ever reported in North America (Quigley and Hornocker 2010). A high density such as this one in the Cypress Hills might make carcass-sharing a more frequent trend.

When utilizing cameras to observe wildlife behaviour at a kill site, cameras should ideally be set up as soon as possible after finding a carcass. I suggest using larger memory cards and checking the cameras more frequently than I did because I missed several days of coverage that might have shown cougars interacting at the carcass. Birds and small mammals will quickly use up camera memory space, and although human scent may deter certain species of wildlife, I found that was not the case with cougars. Wildlife cameras are a reliable and economical substitute for GPS radiocollars, and help us to observe behaviour that we could not detect otherwise.

Figure 1. Cougar 1 scavenging on elk carcass, January 12 2009. This adult female spent most a full week scavenging, grooming and sleeping next to the carcass.

Figure 2. Cougar 2 walking by elk carcass, January 13 2009. This young cougar was never captured eating on camera.

Figure 3. Cougar 3 walking away from elk carcass on January 26 2009, captured on landowners' camera (photo courtesy of D. Mitzner).

Figure 4. The short ears, tail and radiocollar identified this adult female when she visited the elk carcass on March 30 2009.

Figure 5. The obvious size difference of Cougar 5 made him easily recognizable, and helped us confirm the presence of another male cougar in the region.

Figure 6. The third radiocollared female to find the carcass, Cougar 6 scavenged on what little remained of the elk in March 2009.

LITERATURE CITED

Anderson Jr., C. R., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67:307─316.

Bacon, M. M., and M. S. Boyce. 2009. The prairie cougar: Examining the effects of a re-established predator population. Nature Alberta 38:20─23.

Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behaviour in Puma. The Southwestern Naturalist 50:466─471.

Coates, P. S., J. W. Connelly, and D. J. Delehanty. 2008. Predators of Greater Sage-Grouse nests identified by video monitoring. Journal of Field Ornithology 79:421─428.

Cutler, T. L., and D. E. Swann. 1999. Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27:571─581.

George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133:107─117.

Hernández, L., J. W. Laundré, and M. Gurung. 2005. From the field: use of camera traps to measure predation risk in a puma-mule deer system. Wildlife Society Bulletin 33:353─358.

Jacobson, H. A., J. C. Kroll, R. W. Browning, B. H. Koerth, and M. H. Conway. 1997. Infrared-triggered cameras for censusing white-tailed deer. Wildlife Society Bulletin 25:547─556.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852─2862.

Knopff, K. H., A. A. Knopff and M. S. Boyce. 2010. Scavenging makes cougars susceptible to snaring at wolf bait stations. Journal of Wildlife Management 74:644─653.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management 73:586─597.

Logan, K. A., and L. L. Sweanor. 2010. Behaviour and social organization of a solitary carnivore. Pages 105─117 in Cougar ecology and conservation. Edited by M. Hornocker and S. Negri, University of Chicago Press, Chicago, USA.

Logan, K. A., and L. L. Sweanor. 2001. Desert Puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington DC, USA.

Moruzzi, T. L., T. K. Fuller, R. M. DeGraaf, R. T. Brooks, and W. Li. 2002. Assessing remotely triggered cameras for surveying carnivore distribution. Wildlife Society Bulletin 30:380─386.

Nowak, M. C., T. E. Taylor, and G. W. Witmer. 2000. Prolonged scavenging by a female mountain lion in northeastern Oregon. Northwestern Naturalist 81:63─65.

Quigley, H., and M. Hornocker. 2010. Cougar population dynamics. Pages 59─75 in Cougar ecology and conservation. Edited by M. Hornocker and S. Negri, University of Chicago Press, Chicago, USA.

Ross, I. P., and M. G. Jalkotzy. 1996. Cougar predation on moose in southwestern Alberta. Alces 32:1─8.

Stein, A. B., T. K. Fuller, and L. L. Marker. 2008. Opportunistic use of camera traps to assess habitat-specific mammal and bird diversity in northcentral Namibia. Biodiversity Conservation 17:3579─3587.