University of Alberta

GRIZZLY BEAR RESPONSE TO OPEN-PIT MINING IN WESTERN ALBERTA, CANADA

by

Bogdan Cristescu

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

Doctor of Philosophy

in

Ecology

Department of Biological Sciences

Spring 2013
Edmonton, Alberta

ABSTRACT

Industrial development is transforming Alberta's landscapes, with largely unquantified effects on wildlife species. Open-pit mining is occurring on vast expanses, most notably for bitumen but also extensively for coal in a rich seam that traverses the province. Major concerns have developed over the status of the grizzly bear (*Ursus arctos*) in relation to this and other industrial developments, contributing to the species' listing as threatened. My objective was to assess how bears respond to mining by using Global Positioning System (GPS) data from radiocollared individuals. Using movement data in a Before-After-Control-Impact design, I found that bears used mined landscapes during and after mining, selecting undisturbed and reclaimed areas over active and inactive ones. Females with cubs had the greatest home range overlap with mines. Males moved shorter distances on/near mines following reclamation. Based on field visitation of GPS clusters I developed a multinomial model to predict bear behavioural state from GPS radiocollar data. The model had good predictive accuracy particularly for ungulate consumption. Predation is an important source of meat for grizzly bears on mined landscapes, with elk (*Cervus elaphus*) a major component in bear diet following reclamation. Although all ungulates except moose (*Alces alces*) were more likely to occur on reclaimed mines, bears consumed them primarily outside mined areas, or in undisturbed tree patches on mines. Caching of food was common, especially large-bodied prey. Dietary analysis from scat showed that bears switched their diet from predominantly ungulates in the foothills and

Hedysarum spp. roots in the mountains to herbaceous vegetation sown on mines for reclamation. I propose that resting-site selection can be used as an indicator of perceived risk from human 'predation', and show that bears select high horizontal cover for resting, bedding more during the day in foothills with high human activity, and at night on reclaimed mines and in protected areas. Because the mines had restrictions on public access, these findings suggest that bears can persist despite landscape change because they are remarkably adaptable to disturbance and food availability. However, risk of mortality is high if bears are not protected from humans, e.g., by using access management.

ACKNOWLEDGMENTS

The data used for this dissertation is a result of a substantial collaborative effort without which this project would have been impossible. Many people helped tremendously along the years and the ones I thank below are only a fraction of the people who shaped my path along the graduate program at the University of Alberta. I apologize to anyone I may have omitted.

First of all, this work was possible because of the support from my parents, Violeta and Stefan Cristescu, who have encouraged and helped me in countless ways since day 1.

The dedication and commitment of field and lab technicians and volunteers made this field intensive project on grizzly bear ecology possible. I extend many thanks to them, because without their enthusiasm and diligence in data collection this final product would have not been achievable. My feeling and hope are that our work side by side in the field and lab paved the way to future collaborations. These people include Nils Anderson, Ana Balanean, Aurelie Bessiere, Cheyenne Burnett, Kevin Chan, Marine Drouilly, Stacie Evans, Heather Forrest, Emily Hamblen, Quinn Harrison, Richard Hedley, Wee Wei Khoo, Emily Laycock, Alice Qina Li, David Logan, Paul McDonald, Ian McIvor, Elizabeth Milne, David Morgan, Yannick Neveux, Bethany Paul, Patrick Schirf, Chris Sharp, Ayden Sherritt, Autumn Solomon, Kathy Unger, Matthew Urmson, Cara Whalen, Adam Zier-Vogel.

I thank my supervisor, Dr. Mark Boyce for an amazing opportunity to be a part of his research lab. This project, or for that matter my entire experience in Canada, would have not have been possible without him. He is the one to first introduce me to Canadian wilderness in 2007. I am immensely grateful to have benefitted from his mentorship throughout this program. Specifically, I thank him for sharing his immense knowledge in ecology, conservation and statistics, and for providing ample guidance and assistance with fundraising for an expensive, field intensive project. I also thank him for encouraging and financially supporting my attendance to scientific meetings, as well as nominating me for multiple awards throughout my graduate degree. His editorial comments on paper drafts have been invaluable and his recommendation that I be accepted on the North America Board of Directors of the Society for Conservation Biology was a significant stepping stone in my experience. I value and respect his passion and enthusiasm towards wildlife, science and research.

Thank you to my supervisory committee composed of Andrew Derocher, Mark Lewis, and Gordon Stenhouse for excellent support in planning, executing and reporting on the results of this project. I thank them as well as Lee Foote and Sterling Miller for reviewing my thesis and providing necessary feedback.

I also thank many people associated with the Foothills Research Institute Grizzly Bear Program for their invaluable support throughout the duration of this project, whether in the office or field. A special thank you goes to Gordon Stenhouse who has overseen many of the field operations and has provided extensive insights into some of the practicalities of grizzly bear research. His confidence in my abilities was greatly appreciated. Karen Graham, Terry Larsen and Bernie Goski helped enormously with field logistics. Julie Duval and Jerome Cranston provided GIS support.

Many colleagues and friends have helped shape ideas for this project. In particular, discussions with members of the Boyce lab have always been stimulating. Simone Ciuti, Kyle Knopff, and Joe Northrup merit special acknowledgement. In her role as the Boyce lab coordinator, Cathy Shier was extremely helpful on logistical and student life matters.

I am grateful to Kristine Teichman for thoughtful support and stimulating ideas throughout this experience.

Charlene Nielsen provided excellent GIS expertise and Scott Nielsen interesting conversations that improved my knowledge of grizzly bears. Beth MacCallum with Bighorn Wildlife Technologies and John Kansas with Hab-Tech Environmental shared their expertise and long-term knowledge of the study area.

Thank you to John Saunders and Steve Wotton with Peregrine Helicopters for many memorable experiences, including capturing and tracking bears, deploying myself and volunteers in remote areas of the Rockies, trying to save me when thinking I was being attacked by a predatory bear, and taking the crew to safety when our remote campsite was visited by bears. I also thank Sean Biesbroek and Michael Dupuis with Wildlife Air for enabling succcessful telemetry flights, even though at times they took telling photos of me on bumpy days.

I thank Alberta SRD including among others Chris Watson and Brian Voogd, who have supported the project in numerous ways, even after a particularly persistent bear used one of their new culvert traps as a 'boxing sack'. I thank Jasper National Park (Parks Canada) and the people of Cadomin who provided a very hospitable welcoming to their community which served as my field base for the better part of 3 years.

I thank Teck Resources Limited and Sherritt International Corporation for enabling this research on their mineral surface leases, in particular Marc Symbaluk, Leo Paquin and David Brand for interesting discussions and help with orientation and safety on mine sites.

For financial support I gratefully acknowledge the Alberta Conservation Association (fieldwork funding and Research Assistantships), Alberta's Conservation Collaboration, Alberta Ingenuity Fund, Alberta Society of Professional Biologists, Alberta Sport, Recreation, Parks & Wildlife Foundation, American Society of Mammalogists, Athabasca Bioregional Society, Canadian Wildlife Federation, Foundation for North American Wild Sheep – Alberta Chapter, International Association for Bear Research and Management, Mountain Equipment Co-op, Safari Club International – Northern Alberta Chapter, TD Friends of the Environment Foundation, Teck Resources Limited and the University of Alberta (FS Chia Ph.D. Scholarship, Teaching Assistantships).

Finally, I am grateful for being able to work in west-central Alberta in an area and on a project that have been thought provoking and complex, and on such an inspiring study species. The experience has given me a down-to-earth perspective and an even more solid praise for wildlife conservation. I hope that this work will benefit land use planning and environmental mitigation, enabling persistence of grizzly bears and their long-term recovery in Alberta.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION

Rapid human population growth and associated increasing demand for resources set mounting pressure on natural ecosystems. Whether targeting fossil fuels, metals, timber, or even harnessing renewable sources such as through wind or water turbines, or photovoltaic panels, industrial developments modify habitats and can affect wildlife populations (McNeely 1992, Sala et al. 2000, Chow et al. 2003, Northrup and Wittemyer 2013). Modern technologies allow resource exploitation in even the remotest environments such as high alpine, Arctic, or ocean floor. In addition to changing landscapes at the development sites, burning of fossil fuels contributes to climate change, with carbon emissions feeding into biogeochemical cycles at the planetary level (Lashof and Ahuja 1990, Bond et al. 2007, Raupach et al. 2007). The existing network of protected areas may be unable to offset the effects of warming especially if land stewardship outside protected areas is not based on a long-term vision of habitat conservation and restoration (Naidoo and Ricketts 2006, Miles and Kapos 2008, Scharlemann et al. 2010). Protected areas are vital for ensuring core habitats for populations but land-use planning practices outside these will make the difference for species conservation (James et al. 2001; Hansen and Defries 2007; Newmark 2008). With societal values not always aligned with scientific values (Jepson and Canney 2001), many protected areas have been designated for their aesthetical appeal and not necessarily conservation importance. For example, 48% of the land surface area of Banff, Yoho and Kootenay National Parks is unsuitable to grizzly bears (*Ursus arctos*) mainly because it is composed of rock and ice (Gibeau et al. 2001), and establishing protected areas to benefit wildlife as well as people is challenging (Parsons 1995). However, it is typically beyond the boundaries of protected areas that conservation challenges are the greatest and priority research needs to occur (Ogada et al. 2003, Adams et al. 2004, Ceballos et al. 2005).

Understanding the influence of human activity on species and habitats, conservation biology was formed as a crisis discipline (Soule 1985, Meine et al. 2006) meant to inform decision making for conservation. For example, landscape connectivity to promote the movement of mammals between protected areas is a necessity for conservation (Noss et al. 1996, Soule and Terborgh 1999). Although conservation challenges can occur within protected areas, these are often related to human land use outside the protected perimeter (Woodroffe and Ginsberg 1998). Areas lacking protection are generally more at risk of losing their biodiversity value (Pressey et al. 2007) because they are exposed to habitat change and other human pressures (Soule and Sanjayan 1998, Miller and Hobbs 2002, Cox and Underwood 2011). Research programs that link conservation to wildlife behaviour not only will advance these two fields of scientific enquiry, but also will deliver solutions to conservation challenges.

Recent advancements in technology allow tracking of movements and behaviour of wildlife through the use of radio transmitters and/or Global Positioning System (GPS) devices, under increasingly stringent animal-welfare restrictions associated with wildlife capture and handling (Ropert-Coudert and Wilson 2005, Wilson and McMahon 2006). The field of movement ecology is benefitting from wide availability of GPS radiotelemetry (Nathan et al. 2008, Cagnacci et al. 2010), which also was used extensively for this thesis. Other technologies allow acquisition of video footage or still images 'from the animal's perspective' (Moll et al. 2007). Battery life for the latter devices and computation power to process data once retrieved remain major challenges. An example of such novel technology was piloted on the Foothills Institute Grizzly Bear Program (Hinton, Alberta) (Hunter et al. 2007). Animal PathFinder™ units were fitted to GPS radiocollars and deployed on grizzly bears, with the units taking still images every 10 minutes, and recording the 'true' movement trajectory of each animal based on accelerometer, pedometer and compass devices. Such detailed data can provide unprecedented insights into bear behaviour.

Understanding wildlife response to human activity and landscape modification is needed for threatened species with low reproductive rates, at low densities, and with need for seasonal habitats, such as the grizzly bear (Weaver et al. 1996). A dramatic representation of the power of humans to modify landscapes is achieved by open-pit mining. There are a variety of options for mined lands following mine closure (Pearman 2009), one being reclamation to wildlife habitat (Erickson 1995), but at high latitudes and elevations, ecological succession can be lengthy (Smyth 1997). Some species such as forest specialists (e.g., fisher [*Martes pennanti*], Canada lynx [*Lynx canadensis*], American marten [*Martes americana*]) may not colonize these landscapes especially if reclaimed to open vegetation types, whereas ungulates may thrive on these human-modified landscapes (MacCallum and Geist 1992, Jansen et al. 2009). However, little is known about the response of large carnivores to mine reclamation and active mining partly because of rarity, wide-ranging movements, and the difficulty of monitoring these animals. Mining developments are ongoing or planned at localities throughout grizzly bear range in Alberta, British Columbia, Yukon, and Alaska. This alteration of grizzly bear habitats comes at a time when there is concern with widespread decline of this species' range throughout much of North America, primarily as a result of human persecution, habitat loss, and illegal shooting (Mattson and Merrill 2002, Laliberte and Ripple 2004). While predator management has been recently more in favour of predators (Linnell et al. 2001), tipping points (Drake and Griffen 2010, Scheffer 2010), Allee effects (Stephens and Sutherland 1999) and the extinction debt (Tilman et al. 1994) provide solid incentive for researchers to monitor predator populations of conservation concern.

Grizzly bears are considered an umbrella species (Noss et al. 1996) because of their wide ranging patterns, and protecting areas for grizzly bear conservation could in theory protect other species found within bear home ranges. In some places grizzly bears also can be a keystone species, because of their role in seed dispersal, soil aeration through digging for roots (Tardiff and Stanford 1998) and nutrient cycling from aquatic to terrestrial ecosystems through salmon consumption (Gende et al. 2002). Elimination of grizzly bears or other species at top of the food pyramid could trigger trophic cascades, particularly in simple predator-prey systems, whereby increased herbivory as a result of predator disappearance can have repercussions for lower trophic levels (Sergio et al. 2008, Estes et al. 2011). Interior brown bear populations, particularly at northerly latitudes, have a high proportion of meat in their diets, and their impact on ungulate populations can be high (Zager and Beecham 2006, Bojarska and Selva 2011). Based on these considerations, and building on the long-term research by the Foothills Research Institute Grizzly Bear Program, I set out to investigate the effects of mining on grizzly bears with an important direction of research being bear consumption of ungulates in the study area.

The succession of main data chapters is from broad to finer scale, from landscape ecology to behaviour. In Chapter 2, I use long-term data to provide an overview of movement response by grizzly bears to mining. I examine space use, from home-range overlap with mine leases, to length of movement steps depending on mining phase (during versus after mining), mining activity status, and environmental variables. In Chapter 3, I use spatially and temporally referenced bear locations, and bear behaviour information collected over 3 years of fieldwork to separate behavioural states from GPS cluster characteristics. In Chapter 4, I analyze bear feeding comparing diet composition on versus off reclaimed mines, showing that the grizzly bear is an adaptable omnivore that can persist on heavily human modified landscapes, if habitat reclamation incorporates species that can be consumed by bears. Chapter 5 provides an in-depth analysis of ungulate consumption by grizzly bears, in addition to testing hypotheses and assumptions on caching behaviour. In Chapter 6 I propose that choice of resting sites is an indicator of risk-averse behaviour by bears, and information on habitat and timing of this choice could be interpreted as a proxy for perceived risk of 'predation' from humans.

Two Appendices complement the thesis and are tailored towards mining professionals, providing empirical evidence of grizzly bear response to mining.

The Appendices also include suggestions on mitigating the effects of active mining and managing reclaimed mines to facilitate grizzly bear persistence. Appendix 1 documents locations of active haul crossings, and describes bedding and ungulate consumption sites. Appendix 2 includes a broad diet description for bears on mined areas within the study area. Both Appendices describe bear use of the mined landscapes in relation to designated access trails and season. The study areas differ between these two Appendices, with the larger mineral surface lease (MSL) for the first one, and more restricted mineral disturbance limit (MDL) for the second one. Both were published in mining conference proceedings (Appendix 1 - Mine Closure 2011; Appendix 2 - British Columbia Mine Reclamation Symposium 2012).

LITERATURE CITED

Adams, W. M., R. Aveling, D. Brockington, B. Dickson, J. Elliott, J. Hutton, D. Roe, B. Vira, and W. Wolmer. 2004. Biodiversity conservation and the eradication of poverty. Science **306**:1146-1149.

Blumstein, D. T., and E. Fernandez-Juricic. 2004. The emergence of conservation behavior. Conservation Biology **18**:1175-1177.

Bojarska, K., and N. Selva. 2011. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mammal Review **42**:120-143.

Bond, T. C., E. Bhardwaj, R. Dong, R. Jogani, S. Jung, C. Roden, D. G. Streets, and N. M. Trautmann. 2007. Historical emissions of black and organic carbon aerosol from energy-related combustion, 1850-2000. Global Biogeochemical Cycles **21**:GB2018.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2157-2162.

Caro, T. 2007. Behavior and conservation: a bridge too far? Trends in Ecology and Evolution **22**:394-400.

Ceballos, G., P. R. Ehrlich, J. Soberon, I. Salazar, and J. P. Fay. 2005. Global mammal conservation: What must we manage? Science **309**:603-607.

Chow, J., R. J. Kopp, and P. R. Portney. 2003. Energy resources and global development. Science **302**:1528-1531.

Cox, R. L., and E. C. Underwood. 2011. The importance of conserving biodiversity outside of protected areas in Mediterranean ecosystems. PLoS ONE **6**:e14508.

Drake, J. M., and B. D. Griffen. 2010. Early warning signals of extinction in deteriorating environments. Nature **467**:456-459.

Erickson, D. L. 1995. Policies for the planning and reclamation of coal-mined landscapes: An international comparison. Journal of Environmental Planning and Management **38**:453-467.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soule, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of Planet Earth. Science **333**:301-306.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience **52**:917-928.

Gibeau, M. L., S. Herrero, B. N. McLellan, and J. G. Woods. 2001. Managing for grizzly bear security areas in Banff National Park and the Central Canadian Rocky Mountains. Ursus **12**:121-130.

Hansen, A. J., and R. Defries. 2007. Ecological mechanisms linking protected areas to surrounding lands. Ecological Applications **17**:974-988.

Hunter, A. J. S., G. B. Stenhouse, and N. El-Sheimy. 2007. A new technology solution for the study of bear movement and habitat use: The Animal PathFinder™. Paper presented at the 18th International Conference on Bear Research and Management, Monterrey, Mexico.

James, A., K. J. Gaston, and A. Balmford. 2001. Can we afford to conserve biodiversity? BioScience **51**:43-52.

Jansen, B. D., P. R. Krausman, K. D. Bristow, J. R. Heffelfinger, and J. C. deVos, Jr. 2009. Surface mining and ecology of desert bighorn sheep. Southwestern Naturalist **54**:430-438.

Jepson, P., and S. Canney. 2001. Biodiversity hotspots: hot for what? Global Ecology and Biogeography **10**:225-227.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience **54**:123-138.

Lashof, D. A., and D. R. Ahuja. 1990. Relative contributions of greenhouse gas emissions to global warming. Nature **344**:529-531.

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

Linnell, J. D. C., J. E. Swenson, and R. Andersen. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation **4**:345-349.

MacCallum, B. N., and V. Geist. 1992. Mountain restoration: Soil and surface wildlife habitat. GeoJournal **27**:23-46.

Mattson, D. J., and T. Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850 –2000. Conservation Biology **16**:1123-1136.

McNeely, J. A. 1992. The sinking ark: pollution and the worldwide loss of biodiversity. Biodiversity and Conservation **1**:2-18.

Meine, C., M. Soule, and R. F. Noss. 2006. “A mission-driven discipline”: the growth of conservation biology. Conservation Biology **20**:631-651.

Miles, L., and V. Kapos. 2008. Reducing greenhouse gas emissions from deforestation and forest degradation: Global land-use implications. Science **320**:1454-1455.

Miller, J. R., and R. J. Hobbs. 2002. Conservation where people live and work. Conservation Biology **16**:330-337.

Moll, R. J., J. J. Millspaugh, J. Beringer, J. Sartwell, and Z. He. 2007. A new 'view' of ecology and conservation through animal-borne video systems. Trends in Ecology and Evolution **22**:660-668.

Naidoo, R., and T. H. Ricketts. 2006. Mapping the economic costs and benefits of conservation. PLoS Biology **4**:2153-2164.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences, USA **105**:19052-19059.

Newmark, W. D. 2008. Isolation of African protected areas. Frontiers in Ecology and the Environment **6**:321-328.

Northrup, J. M., and G. Wittemyer. 2013. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. Ecology Letters **16**:112-125.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949-963.

Ogada, M. O., R. Woodroffe, N. O. Oguge, and L. G. Frank. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. Conservation Biology **17**:1521-1530.

Parsons, R. 1995. Conflict between ecological sustainability and environmental aesthetics: Conundrum, canard or curiosity. Landscape and Urban Planning **32**:227-244.

Pearman, G. 2009. 101 things to do with a hole in the ground. Post-Mining Alliance. Eden Project, Cornwall, UK.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson. 2007. Conservation planning in a changing world. Trends in Ecology and Evolution **22**:583-592.

Raupach, M. R., G. Marland, P. Ciais, C. Le Quere, J. G. Canadell, G. Klepper, and C. B. Field. 2007. Global and regional drivers of accelerating CO2 emissions. Proceedings of the National Academy of Sciences, USA **104**:10288-10293.

Ropert-Coudert, Y., and R. P. Wilson. 2005. Trends and perspectives in animal-attached remote sensing. Frontiers in Ecology and the Environment **3**:437-444.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B.

H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Scharlemann, J. P. W., V. Kapos, A. Campbell, I. Lysenko, N. D. Burgess, M. C. Hansen, H. K. Gibbs, B. Dickson, and L. Miles. 2010. Securing tropical forest carbon: the contribution of protected areas to REDD. Oryx **44**:352-357.

Scheffer, M. 2010. Foreseeing tipping points. Nature **467**:411-412.

Sergio, F., T. Caro, D. Brown, B. Clucas, J. Hunter, J. Ketchum, K. McHugh, and F. Hiraldo. 2008. Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. Annual Review of Ecology Evolution and Systematics **39**:1-19.

Smyth, C. R. 1997. Early succession patterns with a native species seed mix on amended and unamended coal mine spoil in the Rocky Mountains of Southeastern British Columbia, Canada. Arctic and Alpine Research **29**:184-195.

Soule, M. E. 1985. What is conservation biology? BioScience **35**:727-734.

Soule, M. E., and M. A. Sanjayan. 1998. Conservation targets: Do they help? Science **279**:2060-2061.

Soule, M. E., and J. Terborgh. 1999. Conserving nature at regional and continental scales-a scientific program for North America. BioScience **49**:809-817.

Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology and Evolution **14**:401-405.

Tardiff, S. E., and J. A. Stanford. 1998. Grizzly bear digging: Effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology **79**:2219-2228.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371**:65-66.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10**:964-976.

Wilson, R. P., and C. R. McMahon. 2006. Measuring devices on wild animals: what constitutes acceptable practice? Frontiers in Ecology and the Environment **4**:147-154.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science **280**:2126-2128.

Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. Ursus **17**:95-108.

CHAPTER 2

MINING DEVELOPMENT AND RECLAMATION ALTER GRIZZLY BEAR MOVEMENTS

ABSTRACT

Increasing global energy demands have resulted in widespread proliferation of resource extraction industries even in remote areas with historically low human footprint. This rapid expansion requires effective means of appraising landscape change effects on wildlife populations. I used a 9-year movement dataset from grizzly bears (*Ursus arctos*) (*n* = 18) monitored with GPS radiocollars in Alberta, Canada to assess bear space use during active mining operations versus after mine closure and reclamation. Grizzly bear home range overlap with mined areas was lower during the active mining stage except for females with cubs. This reproductive class also had shorter movements when in areas with active mining, suggesting habituation to mining activity, cautious movements, or possibly a mechanism to avoid infanticidal males. Males either avoided mines at the active phase, or had longer movements in active mining areas. However, at the broader landscape level, both females with cubs and males made shorter steps when on/close to mines after mine reclamation. Controlling for bear movements beyond a 7.2 km buffer around mineral disturbance limits revealed that movement rates of bears from all reproductive classes were affected by mine closure. Following reclamation, males had shorter movements likely indicative of grazing, whereas females had longer steps indicative of unrestricted movements in the absence of active coal extraction/hauling, or potentially flight response upon male detection. The results show differences in bear space-use strategies by reproductive status and mining phase, with a key population segment (females with cubs) appearing most adaptable to mining during both active and reclaimed phases.

INTRODUCTION

Movement is the underlying mechanism that determines the redistribution of vagile organisms on the landscape in response to environmental cues, including human-caused disturbances. Our increased ability to track animal movement enables insights into behavioural responses to human-induced landscape modification, even for animals otherwise difficult to study because of their rarity, wide ranging patterns and/or inhospitable study environments (Nathan et al. 2008, Cagnacci et al. 2010). When used in conjunction with animal space use, such as home range patterns, information on movement behaviour can assist land-use planning decisions that promote animal persistence, including designating areas for conservation and ensuring movement connectivity (Noss et al. 1996, Minor and Lookingbill 2010).

When an animal movement trajectory is sampled, a variety of simple movement metrics can be calculated (Turchin 1998), with one of the most common being step length. Levy flights (Viswanathan et al. 1996) or fractal dimension (Nams and Bourgeois 2004) can be used to model the distribution of step lengths, with Levy-modulated random walks sometimes having good concordance with real data (Ramos-Fernandez et al. 2004, Dai et al. 2007). Random walk models can be parameterized with theoretical distribution such as exponential decay (Codling et al. 2008), but using step lengths tailored to the study organism/question to inform random walks can provide more informative simulations of animal movement (Whittington et al. 2004). In addition, step-length distributions can be used to model relative probability of step selection, contrasting variables hypothesized to affect movement along used and available movement paths (Fortin et al. 2005). Step length also has been related to feeding habits (Edwards et al. 2011), broad human disturbance, and temporal activity patterns (Boyce et al. 2010), as well as bold and shy personality types (Ciuti et al. 2012). At fine scale, distance moved by an animal in response to disturbance has been quantified to assess fear response to humans (Stankowich 2008).

In Alberta, Canada, accelerated development of natural resource extraction is occurring concomitant with disruption of native landscapes. Rapid landscape change can also result in increased human access and can be detrimental to wildlife, contributing for example to the listing of the grizzly bear (*Ursus arctos*) as threatened in Alberta (Alberta Grizzly Bear Recovery Team 2008). Open-pit mining is arguably the most invasive of these extractive industries, with Alberta being known worldwide for oil sands exploitation. Surface mining for coal on the other hand is not as widely publicized but coal mining operations are also experiencing rapid expansion in response to global demand for hydrocarbons. Irrespective of targeted below ground resource, open-pit mining has substantial potential to alter animal movement through large scale habitat destruction. During active mining, natural vegetation is stripped, the soil layer is removed and blasting operations expose target mineral deposits sometimes located hundreds of metres below the original land surface. Mined landscapes are drastically disturbed sites hosting a complex array of features including active and inactive pits, haul roads used by heavy machinery, processing plant(s), offices, and tailing ponds.

While mined areas may not seem like an environment conducive for wildlife persistence, following mine closure reclamation efforts often aim to create wildlife habitat. The extent to which mined areas affect animal distribution is known for a number of ungulate species (MacCallum and Geist 1992, Weir et al. 2007, Jansen et al. 2009), but even the most basic information is lacking on the effects of mining on facultative or obligate carnivores at top of the food chain. This scarcity of knowledge is partly caused by the difficulty of capturing and monitoring these animals, as well as possibly due to researchers choosing not to undertake studies on heavily disturbed sites such as open-pit mines, under the assumption that top predators as biodiversity indicators (Sergio et al. 2006) and umbrella species (Sergio et al. 2008) are unlikely to contribute to ecosystem function on mined lands. However, such assumptions have been challenged at local scales (Ordenana et al. 2010, Carter et al. 2012) as well as continental level (Linnell et al. 2001). Minimizing human persecution and indirect effects of human activity on carnivore populations, such as human-caused changes in prey (Weaver et al. 1996, Hayward 2009), remain major challenges. Perceived 'predation' risk from humans could have fitness costs for predators including decreased food intake and altered reproductive success. On a mining landscape, detailed dietary analysis for grizzly bears showed bears feeding on vegetation used for reclamation purposes (Chapter 4, Cristescu et al. 2012) but additional metrics are required to understand finer scale effects of mining on bears, such as potential trade-offs between feeding and safety under the risk of human 'predation'.

At the onset of my assessment of mining effects on grizzly bear movements, I expected no bear use of the mine sites during the active mining phase because of high levels of human activity at the sites. Conversely, based on the ability of bears to colonize other human-disturbed areas such as logging cutblocks (Nielsen et al. 2004), I expected that bear home ranges might include the mine sites after mine closure. Using step length (movement rate) as a surrogate for bear response to perceived risk of 'predation' from humans, I anticipated that bear movement steps starting in active mining areas would be longer than those in undisturbed areas (tree patches) on mines, reflecting a flight response. I also hypothesized that more steps would be confined to mining boundaries after mining than during the active mining phase. Crossing an operational haul road was expected to trigger changes in step length and habitat use through which bears travel. Following mine closure, reclaimed mine land within the study area had little human access but high bear food availability (Chapter 4). Because step length is indicative not only of response to risk factors but also feeding, I expected step length after mine reclamation to be shorter if starting on or near mines. My study followed a Before-After-Control-Impact (BACI) design (Stewart-Oaten et al. 1986, McDonald et al. 2000), where the ‘Control’ included bear movements in undisturbed areas.

METHODS

Study Area and Design

I carried out the study in a 538 km^2 primary study area and surrounding region located in west-central Alberta, Canada (approximate central coordinates 53°05' N 117°25' W) (Figure 2.1). The area has complex topography and land cover, including foothills and the eastern slopes of the Rocky Mountains (elevation; mean ± SD, 1,981 ± 460 m). Natural vegetation cover is dominated by boreal forest composed of lodgepole pine (*Pinus contorta*), white (*Picea glauca*) and black spruce (*P. mariana*), balsam fir (*Abies balsamea*) and subalpine fir (*A. lasiocarpa*). Mixed and deciduous forest patches dominated by balsam polar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*) are uncommon. Shrub cover is dominated by willow (*Salix* spp.), dwarf birch (*Betula* spp.) and alder (*Alnus* spp.). Grasslands are primarily human-generated and present on mineral disturbance limits (hereafter, MDLs) to variable extents depending on reclamation stage of the two neighbouring open-pit coal mines under study (Luscar and Gregg River, combined MDL 41.6 km^2). Barren (non-vegetated) land is present on mines as a result of mining operations and includes pit walls, rock piles/dumps and wide mining roads. Barren land also is naturally present at high elevation where climatic conditions make it difficult for vascular plants to develop.

The primary area includes the MDL and adjacent lands up to a distance of 7,240 m from the boundaries of the two neighbouring mines. The spatial extent was obtained through buffering the combined MDL of the two mines by a distance equal to the 95th percentile of the greatest step length of GPS radiocollared grizzly bears which used the MDL at least once in the monitoring period (n = 18) (detail on grizzly bear data in Supplementary material). Grizzly bears in the region persist at one of the lowest densities recorded for the Alberta threatened grizzly bear population (Boulanger et al. 2005). An additional coal mine (Cheviot) located 7.9 km away from the other two mines was active during 2004-2010 but was not considered for statistical modeling because of small associated bear movement sample sizes. However, the Cheviot mine haul road section located outside MDL boundaries (10.6 km) linking Cheviot active pits to a coal processing plant on Luscar mine was included in analyses. County roads (primarily gravel) present in the area have unrestricted use whereas public access is prohibited on mine haul roads. The latter accommodate a range of vehicle sizes including heavy coal haul trucks. Human recreational activities and to a smaller extent gas exploration and logging occur within the study area buffer outside MDLs. Access is not allowed within MDLs except during the reclamation phase along a few restricted trails.

Gregg River mine closed in 2004 and operations at the neighbouring Luscar mine were much reduced after that year, involving overburden dumping and sloping/soil placement in small restricted areas, with coal haul occurring along a haul road from Cheviot mine. I therefore partitioned the analyses in two periods using a Before-After-Control-Impact design, contrasting bear movements during (1999-2003) and after (2005-2010) active mining phases. I then carried out a suite of spatial analyses on grizzly bear movement primarily based around step-length modeling, using STATA v.11.2 (StataCorp, College Station, Texas) and an alpha level of 0.1 because of expected variability affecting lengths of movement steps. Habitat security and food features hypothesized *a priori* to potentially influence bear movements are provided in Table 2.1 (detail on Study design and GIS data as well as modeling and BACI procedure in Supplementary material).

RESULTS

Grizzly bears of all reproductive statuses used the mining area delineated by the MDL during and after the active mining phase. Mean home range overlap with the MDL was low for males (number of individuals; mean ± SD, during: 2.9 ± 0.7 km^2, n = 3; after: 10.3 ± 5.2 km^2, n = 2) and single females (during: 9.6 ± 9.3 km^2, n = 3; after: 10.3 ± 2.8 km^2, n = 4), but high for females with cubs (during: 21.8 ± 8.2 km^2, n = 3; after: 20.2 ± 4.5 km^2, n = 3). Males had low overlap during compared to after mining (Figure 2.2). Grizzly bears in all reproductive classes selected undisturbed (original tree patches) and reclaimed areas within MDLs whether during or after mining, but with less variability in selection patterns in the latter phase (Figure 2.3). Strong selection for undisturbed areas and moderately strong selection for reclaimed areas held consistently across reproductive classes in the after mining phase. Nonetheless, in both mining phases bears generally used areas with active mining operations as well as inactive areas heavily disturbed by mining that provided no vegetative foods.

Some bears were more likely to take longer steps when movement started in an area with active mining operations (Table S.2), but this pattern held at the population level only for single females in the after mining phase and for the only male included in analysis for the during mining phase (Table 2.2). Conversely, females with cubs took shorter steps from active mining polygons compared to steps from undisturbed areas during mining. After mining, females with cubs took longer steps from inactive and reclaimed areas than they did from undisturbed areas. Steps from reclaimed polygons also were longer than those from forest areas within the MDL for single females.

Irrespective of mining phase, bears had a higher proportion of movement steps that crossed the MDL boundaries than steps that stayed within MDL boundaries. The one exception occurred in the after-mining phase for females with cubs, which had an equal proportion of crossing and within-MDL steps (Figure 2.4). However, frequency of steps differed by mining phase for males ($\chi^2 = 21.05$, $df = 1$, $P < 0.0001$), females ($\chi^2 = 13.14$, $df = 1$, $P = 0.0003$) and females with cubs ($\chi^2 = 16.55$, $df = 1$, $P < 0.0001$), with a pattern of more movements within MDLs after mining.

Males ($n = 3$) crossed the location of the haul road before haul road construction but no male crossing by sampled individuals was recorded during the haul road active phase. Single females ($n = 1$) and females with cubs ($n = 2$) crossed the road in the before active haul road phase, and also during active coal hauling (single females: $n = 3$; females with cubs: $n = 2$). Although slightly higher for the latter, female step length did not differ significantly before (mean ± SE, 1775 ± 366 m) versus during (2376 ± 284 m) haul road activity (two-sample Wilcoxon rank-sum, $z = -1.408$, $P = 0.159$). Length weighted mean distances from haul road during crossings steps were greater for females during the active mining phase (651 ± 102 m) compared to before haul road construction (399 ± 109 m) (two-sample Wilcoxon rank-sum, $z = -1.716$, $P = 0.086$). Length weighted mean distances along steps from forest edge was slightly greater before (120 ± 26 m) versus during (83 ± 8 m) haul road activity but the difference was not statistically significant (two-sample Wilcoxon rank-sum, $z = 1.210$, $P = 0.226$). Also in relation to haul-road operation, female bears did not move in steeper terrain before (0.168 ± 0.01 ruggedness) compared to during (0.170 ± 0.01 ruggedness) hauling activity (two-sample Wilcoxon rank-sum, $z = -0.616$, $P = 0.538$).

Mine closure caused a significant change in bear movements for males (BACI, $t = 7.93$, $df = 1383$, $P < 0.0001$), females (BACI, $t = -37.59$, $df = 3232$, $P < 0.0001$), and females with cubs (BACI, $t = 31.93$, $df = 1858$, $P < 0.0001$). Contrasting bear movement rates within a 7.2 km buffer from the MDL during versus after mining, while accounting for lengths of steps occurring beyond 7.2 km (control), showed differential response to mining by bear reproductive status. Males had shorter steps within the buffer after mining compared to during mining operations. Females with/without cubs had longer steps within the buffer after as opposed to during active mining. Models incorporating bear steps occurring within the buffer did not effectively predict population-level step length during the mining phase (Table 2.3). However, when step length was analyzed after mining, distance to MDL at the start location of the step was the variable for which the confidence intervals did not overlap zero most consistently, with closer distance corresponding to shorter steps for males and females with cubs, but not for single females (Table 2.4). However, there was substantial variability in step length for individual bears within a given reproductive status depending on distance to MDL (Figure 2.5). Open land cover type at start location corresponded to longer steps for single females, and steps of females with cubs that started close to major roads were more likely to be shorter (Table 2.4).

DISCUSSION

Extensive industrial development activities are transforming Alberta's landscapes. To assist impact assessments and implement environmental mitigation strategies, we must first document if industry is influencing the space use and behaviour of wildlife. I assessed how the grizzly bear, a flagship and umbrella species threatened in Alberta, is coping with the dramatic change caused by open-pit coal mining over extensive areas of the province. To my knowledge, this study represents the first detailed assessment of carnivore space use in relation to mining areas and at different mining stages. Contrary to expectations, grizzly bear home ranges overlapped mine sites during both mining phases, with the greatest overlap recorded for females with cubs. The latter result, combined with short female with cub movements when starting in an active mining area (during phase), as well as larger proportion of movements within versus simply crossing mines, suggest habituation to industrial activity and tolerance towards human disturbance. Strategies employed by females with cubs to navigate a risky landscape with pit blasting, shoveling, coal and overburden removal and transport might require short movements, which are associated with 'hiding' behaviours and shy personality traits (Ciuti et al. 2012).

Given that males had greater home range overlap and shorter steps on/near mines following reclamation, whereas female were present on mined areas during and after active mining, it is possible that mining could influence the incidence of encounters between males and females with cubs. Concentrated movements on reclaimed mines for grazing on introduced legumes suggest a risk for females with cubs to encounter possible infanticidal males, which could work against the goal of reclamation to enhance wildlife populations. Although data on outcomes of such encounters is lacking for my study population, infanticide by males can impact cub survival in brown bear populations (Swenson et al. 1997, Wielgus and

Bunnell 2000). Longer steps of females following reclamation (when a control area was considered) might indicate flight response upon detection of a possible danger such male bear, or human trail user (Moen et al. 2012). Alternatively, they could indicate movements that are unconstrained by active mining operations, allowing bears of all reproductive classes to effectively graze on herbaceous material sown on mines as part of reclamation. I suggest the need to further study the relationship between males and female with cubs on industrially reclaimed landscapes that change food distribution, at the minimum by monitoring cub survival.

To access reclaimed areas that provided herbaceous forage (primarily legumes and monocots cultivated as part of reclamation), bears needed to cross inhospitable areas dominated by barren rock and/or used by mining activity. However, areas with high human activity can provide refuge for prey species (Muhly et al. 2011, Rogala et al. 2011). In my study system, inactive pit walls on the mine sites are used by bighorn sheep (*Ovis canadensis*) as escape terrain (MacCallum and Geist 1992) and some individual bears may be seeking access to this protein-rich resource. Nonetheless, most bears selected undisturbed tree patches when within the MDL, even at the after mining stage when direct human disturbance was minimal. Such patches possibly facilitate thermal comfort when used for bedding, and provide opportunities to surprise ungulates (Chapters 5-6).

I was unable to ascertain whether the lack of male crossing of the Cheviot haul road during active operation has biological reasons, or is due to sample size limitations regarding number of male bears monitored. In the broader study region, females cross roads more frequently than males (Graham et al. 2010), whereas major highways are crossed by males but not by females (Proctor et al. 2012). The more directional movement of females when crossing an active haul road, as compared to movement in the absence of the haul road, suggests a slight avoidance of mining traffic.

Females with cubs moved shorter distances when in the vicinity of main public roads than when far from roads, suggesting cautious movements even if bears may be exploiting vegetative foods near roads (Roever et al. 2008). These results corroborate the response of females with cubs to roads used by petrocarbon and logging industries (McLellan and Shackleton 1988) but are opposite the findings in the Gibeau et al. (2002) study, where females were the most risk averse to vehicular traffic.

Our framework of predicting bear step length can provide an objective method of identifying zones of influence around disturbances such as open-pit mines, as opposed to assigning arbitrary cut-offs to various disturbance types (e.g., industrial, recreational, residential). For example, for the coal mines under study, environmental impact assessments set the zone of influence at 1 km, without explicit consideration of grizzly bear movements in relation to mining.

Grizzly bears inhabiting a landscape heavily impacted by large scale industrial development used mines during and after active mining operations, with females and their cubs appearing to be the most adaptable. While bears were able to persist on and near mines, their movements were affected by mining. Wilderness areas surrounding mines (including a provincial and national park) likely buffer the effects of mining, and no bear home range occurred entirely within the perimeter of mineral disturbances. Although bears moved in active and inactive areas, reclaimed and especially undisturbed areas on mine sites were strongly selected, suggesting the importance of maintaining original tree patches in mine planning. Reclamation schemes that have habitat creation as end goal, therefore planting vegetative foods to attract wildlife, should incorporate enforcement of human access restrictions to diminish the potential of mine sites becoming ecological traps.

LITERATURE CITED

Alberta Grizzly Bear Recovery Team. 2008. Alberta Grizzly Bear Recovery Plan 2008-2013. [online] URL: http://www.srd.alberta.ca/fishwildlife/wildlifeinalberta/grizzlybearmanagement/default.aspx

Boulanger, J., G. B. Stenhouse, M. Proctor, S. Himmer, D. Paetkau, and J. Cranston. 2005. 2004 Population inventory and density estimates for the Alberta 3B and 4B Grizzly bear management area. Report prepared for Alberta Sustainable Resource Development, Fish and Wildlife Division. Integrated Ecological Research, Nelson, BC, Canada.

Boyce, M. S., J. Pitt, J. M. Northrup, A. T. Morehouse, K. H. Knopff, B. Cristescu, and G. B. Stenhouse. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2213-2219.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2157-2162.

Carter, N. H., B. K. Shrestha, J. B. Karki, N. M. B. Pradhan, and J. Liu. 2012. Coexistence between wildlife and humans at fine spatial scales. Proceedings of the National Academy of Sciences. Online Early doi: 10.1073/pnas.1210490109

Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce. 2012. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society B: Biological Sciences **279**:4407-4416.

Codling, E. A., M. J. Plank, and S. Benhamou. 2008. Random walk models in biology. Journal of The Royal Society Interface **5**:813-834.

Cristescu, B., G. Stenhouse, M. Symbaluk, and M. S. Boyce. 2012. Ecological effects of mine reclamation on grizzly bears. Proceedings of the 36th annual British Columbia mine reclamation symposium, Kamloops BC, September 17-20, 2012. The British Columbia Technical and Research Committee on Reclamation. Bitech Publishers Ltd., Richmond, BC, Canada.

Dai, X., G. Shannon, R. Slotow, B. Page, and K. J. Duffy. 2007. Short-duration daytime movements of a cow herd of African elephants. Journal of Mammalogy **88**:151-157.

Edwards, M. A., A. E. Derocher, K. A. Hobson, M. Branigan, and J. A. Nagy. 2011. Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic. Oecologia **165**:877-889.

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.

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

Graham, K., J. Boulanger, J. Duval, and G. Stenhouse. 2010. Spatial and temporal use of roads by grizzly bears in west-central Alberta. Ursus **21**:43-56.

Hayward, M. W. 2009. The need to rationalize and prioritize threatening processes used to determine threat status in the IUCN Red List. Conservation Biology **23**:1568-1576.

Jansen, B. D., P. R. Krausman, K. D. Bristow, J. R. Heffelfinger, and J. C. deVos, Jr. 2009. Surface mining and ecology of desert bighorn sheep. Southwestern Naturalist **54**:430-438.

Linnell, J. D. C., J. E. Swenson, and R. Andersen. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation **4**:345-349.

MacCallum, B. N., and V. Geist. 1992. Mountain restoration: Soil and surface wildlife habitat. GeoJournal **27**:23-46.

McDonald, T. L., W. P. Erickson, and L. L. McDonald. 2000. Analysis of count data from Before-After Control-Impact Studies. Journal of Agricultural, Biological, and Environmental Statistics **5**:262-279.

McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries - Effects of roads on behavior, habitat use and demography. Journal of Applied Ecology **25**:451-460.

Minor, E. S., and T. R. Lookingbill. 2010. A multiscale network analysis of protected-area connectivity for mammals in the United States. Conservation Biology **24**:1549-1558.

Moen, G. K., O.-G. Stoen, V. Sahlen, and J. E. Swenson. 2012. Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. PLoS ONE **7**:e31699.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PLoS ONE **6**: e17050.

Nams, V. O., and M. Bourgeois. 2004. Fractal analysis measures habitat use at different spatial scales: an example with American marten. Canadian Journal of Zoology **82**:1738-1747.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences, USA **105**:19052-19059.

Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004. Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management **199**:51-65.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949-963.

Ordenana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Siudyla, C. D. Haas, S. Harris, S. A. Hathaway, G. M. Turschak, A. K. Miles, and D. H. Van Vuren. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy **91**:1322-1331.

Proctor, M. F., D. Paetkau, B. N. McLellan, G. B. Stenhouse, K. C. Kendall, R. D. Mace, W. F. Kasworm, C. Servheen, C. L. Lausen, M. L. Gibeau, W. L. Wakkinen, M. A. Haroldson, G. Mowat, C. D. Apps, L. M. Ciarniello, R. M. R. Barclay, M. S. Boyce, C. C. Schwartz, and C. Strobeck. 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. Wildlife Monographs **180**:1-46.

Ramos-Fernandez, G., J. L. Mateos, O. Miramontes, G. Cocho, H. n. Larralde, and B. r. Ayala-Orozco. 2004. Levy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). Behavioral Ecology & Sociobiology **55**:223-230.

Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2008. Grizzly bears and forestry - I: Road vegetation and placement as an attractant to grizzly bears. Forest Ecology and Management **256**:1253-1261.

Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. Ecology and Society **16**. [online] URL: http://dx.doi.org/10.5751/ES-04251-160316

Sergio, F., I. Newton, L. Marchesi, and P. Pedrini. 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. Journal of Applied Ecology **43**:1049-1055.

Sergio, F., T. Caro, D. Brown, B. Clucas, J. Hunter, J. Ketchum, K. McHugh, and F. Hiraldo. 2008. Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. Annual Review of Ecology Evolution and Systematics **39**:1-19.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation **141**:2159-2173.

Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: "Pseudoreplication" in time? Ecology **67**:929-940.

Swenson, J. E., F. Sandegren, A. Soderberg, A. Bjarvall, R. Franzen, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. Nature **386**:450-451.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371**:65-66.

Turchin, P. 1998. Quantitative analysis of movement: Measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, MA, USA.

Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. 1996. Levy flight search patterns of wandering albatrosses. Nature **381**:413-415.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10**:964-976.

Weir, J. N., S. P. Mahoney, B. McLaren, and S. H. Ferguson. 2007. Effects of mine development on woodland caribou *Rangifer tarandus* distribution. Wildlife Biology **13**:66-74.

Whittington, J., C. C. St Clair, and G. Mercer. 2004. Path tortuosity and the permeability of roads and trails to wolf movement. Ecology and Society **9**. [online] URL: http://www.ecologyandsociety.org/vol9/iss1/art4/

Wielgus, R. B., and F. L. Bunnell. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. Biological Conservation **93**:145-154.

Table 2.1: Remote sensing and GIS covariates used for modelling grizzly bear step length in response to open-pit mining in west-central Alberta, Canada. These covariates were hypothesizes to be linked to perceived security, with the study area extent set within a 7.24 km buffer from the mineral disturbance limits (MDLs).

Model variable	**Variable code**	**Variable type**	**Unit/Scale**	**Range**
Land cover				
Closed (forest)	Cov1	Categorical	n.a.	0 or 1
Open (shrub, grass, barren)	Cov2	Categorical	n.a.	0 or 1
Distance to edge	Dedge	Non-linear	Meter	0−1,449
Terrain ruggedness index	TRI	Non-linear	Unitless	0−0.583
Distance to main road	Droad	Non-linear	Meter	0−11,376
Distance to MDL	Dmdl	Non-linear	Meter	0−7,261
Open × Distance to MDL	Cov2 × Dmdl	Linear	Meter	0−7,261

Table 2.2: Predicted population-level grizzly bear step length as a function of mining status at Luscar and Gregg River open-pit coal mines, Alberta, Canada (1999-2003, 2006; 2008-2010 data). GLM-based predictions included 'long' steps not associated with ungulate consumption or bedding behaviours as identified from GPS cluster investigations (step length by reproductive status: males ≥160 m, females ≥146 m, female with cubs ≥154 m). Significant terms are given in bold. Steps staring in the undisturbed mining category were withheld as base category. No reporting of coefficients corresponds to no steps starting in the respective mine activity class.

Model variable	**Reproductive status**								
	Male			Female			Female w/ cubs		
	β_i	90% CI		β_i	90% CI		β_i	90% CI	
During mining									
Intercept	**5.236**	**4.619**	**5.853**	**5.604**	**4.163**	**7.044**	**5.838**	**5.290**	**6.386**
Active	**1.841**	**0.397**	**3.285**	1.109	−0.786	3.004	**−0.298**	**−0.346**	**−0.249**
Inactive	**3.061**	**2.155**	**3.966**	0.357	−0.863	1.576	0.833	−0.115	1.782
Reclaimed	**0.849**	**0.179**	**1.518**	0.699	−0.357	1.754	0.066	−1.153	1.284
After mining									
Intercept	**6.064**	**5.554**	**6.573**	**5.463**	**5.119**	**5.807**	**5.493**	**5.310**	**5.676**
Active				**1.320**	**0.473**	**2.167**	−0.843	−2.230	0.544
Inactive	1.911	−0.150	3.971	0.711	−0.044	1.467	**0.544**	**0.050**	**1.038**
Reclaimed	−0.082	−0.655	0.492	**0.740**	**0.308**	**1.171**	**0.528**	**0.444**	**0.612**

Table 2.3: GLM-based predicted population-level step length of grizzly bears as a function of habitat security features (during mining versus control). Movement data were collected during 1999-2003 in west-central Alberta. 'During mining' steps occurred within a 7.24 km buffer from mine disturbance limits, whereas 'Control' steps were recorded beyond 7.24 km. Parameter estimates correspond to 'long' steps not associated with confined bear activity such as ungulate consumption or bedding. Terms for which confidence intervals do not overlap zero are given in bold. Closed (forest) land cover was witheld as reference category.

Model variable	**Reproductive status**								
	Male			Female			Female w/ cubs		
	β_i	90% CI		β_i	90% CI		β_i	90% CI	
During mining									
Intercept	**6.513**	**4.928**	**8.097**	**6.194**	**5.799**	**6.589**	**6.184**	**5.344**	**7.024**
TRI	−1.568	−4.082	0.946	0.616	−3.121	4.354	3.039	−1.926	8.004
TRI^2	1.562	−0.770	3.894	−6.467	−17.991	5.056	−17.583	−46.149	10.983
Cov2	0.111	−0.050	0.272	0.060	−0.078	0.199	−0.097	−0.296	0.102
Dedge	−0.182^	−0.369	0.004	0.223^	−0.147	0.592	1.119^	−0.725	2.963
Dedge^2	0.215^^	−0.035	0.465	−0.037^^	−0.683	0.609	−2.919^^	−7.730	1.893
Dmdl	−0.156^	−0.488	0.177	0.139^	−0.009	0.287	−0.084^	−0.272	0.104
Dmdl^2	0.017^^	−0.023	0.057	−0.018^^	−0.038	0.002	0.007^^	−0.002	0.002
Droad	0.062^	−0.045	0.170	0.029^	−0.022	0.080	0.007^	−0.043	0.057
Droad^2	−0.005^^	−0.015	0.004	−0.002^^	−0.005	0.002	0.003^^	−0.005	0.011
Cov2 × Dmdl	−0.019^	−0.089	0.051	−0.006^	−0.044	0.032	0.027^	−0.011	0.065
Control									
Intercept	**5.793**	**5.173**	**6.413**	**6.870**	**4.989**	**8.750**	**6.400**	**6.260**	**6.540**
TRI	**4.541**	**0.223**	**8.860**	0.988	−0.533	2.509	−3.633	−9.609	2.343
TRI^2	−18.394	−37.348	0.560	−5.195	−13.427	3.038	19.651	−12.675	51.976
Cov2	0.229	−0.121	0.579	−0.011	−1.649	1.628	−0.085	−0.236	0.066
Dedge	−0.024^	−0.249	0.201	**−0.995^**	**−1.657**	**−0.332**	1.497^	−0.965	3.959
Dedge^2	**0.278^^**	**0.391**	**0.947**	**1.843^^**	**0.008**	**3.678**	−4.329^^	−11.451	2.792
Dmdl	0.035^	−0.022	0.092	−0.302^	−0.758	0.153	0.055^	−0.036	0.146
Dmdl^2	−0.000^^	−0.000	0.000	0.019^^	−0.005	0.043	−0.003^^	−0.008	0.002
Droad	**0.094^**	**0.015**	**0.173**	0.005^	−0.039	0.049	0.062^	−0.006	0.130
Droad^2	**−0.006^^**	**0.012**	**0.001**	−0.001^^	−0.005	0.003	−0.004^^	−0.014	0.005
Cov2 × Dmdl	−0.000^	−0.002	0.002	−0.004^	−0.193	0.185	0.011^	−0.007	0.028

^ Coefficient reported at 10^3 times its actual value; ^^ Coefficient reported at 10^6 times its actual value

Table 2.4: GLM-based predicted population-level step length of grizzly bears as a function of habitat security features (after mining versus control). Movement data were collected during 2006 and 2008-2010 in west-central Alberta. 'After mining' steps occurred within a 7.24 km buffer from mine disturbance limits, whereas 'Control' steps were recorded beyond 7.24 km. Parameter estimates correspond to 'long' steps not associated with confined bear activity such as ungulate consumption or bedding. Terms for which confidence intervals do not overlap zero are given in bold. Closed (forest) land cover was witheld as reference category.

Model variable	**Reproductive status**								
	Male			Female			Female w/ cubs		
	β_i	90% CI		β_i	90% CI		β_i	90% CI	
After mining									
Intercept	**6.971**	**6.331**	**7.610**	**6.833**	**6.079**	**7.587**	**3.522**	**3.082**	**3.962**
TRI	0.150	−0.044	0.344	−2.823	−8.223	2.578	−1.672	−4.421	1.078
TRI^2	−2.708	−6.186	0.770	2.118	−13.667	17.903	3.360	−2.167	8.886
Cov2	−0.184	−0.374	0.011	**0.028**	**0.002**	**0.053**	0.004	−0.003	0.011
Dedge	0.038^	−0.033	0.109	0.231^	−0.219	0.681	0	0	0
Dedge^2	−0.194^^	−0.498	0.110	−0.278^^	−0.934	0.378	0	0	0
Dmdl	**0.261^**	**0.002**	**0.520**	0.148^	−0.048	0.344	**0.027^**	**0.004**	**0.050**
Dmdl^2	−0.043^^	−0.091	0.005	−0.019^^	−0.042	0.003	**−0.005^^**	**−0.008**	**−0.001**
Droad	−0.084^	−0.209	0.042	0.043^	−0.027	0.113	**0.020^**	**0.002**	**0.037**
Droad^2	0.004^^	−0.002	0.011	−0.002^^	−0.004	0.001	−0.006	−0.016	0.003
Cov2 × Dmdl	−0.005^	−0.016	0.006	−0.001^	−0.004	0.002	0.008	−0.005	0.021
Control									
Intercept	**3.871**	**3.137**	**4.604**	6.125	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
TRI	−0.090	−0.239	0.058	0	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
TRI^2	0.182	−0.117	0.481	0	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
Cov2	−0.097	−0.256	0.062	0.137	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
Dedge	0.022^	−0.014	0.058	0	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
Dedge^2	−0.008^^	−0.021	0.005	0	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
Dmdl	**0.222^**	**0.080**	**0.364**	0	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
Dmdl^2	**−0.005^^**	**−0.009**	**−0.002**	0	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
Droad	0	0	0	0.272^	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
Droad^2	0	0	0	−0.014^^	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}
Cov2 × Dmdl	0.001^	−0.001	0.003	0	NA$^+$	NA$^+$	NA^{++}	NA^{++}	NA^{++}

^ Coefficient reported at 10^3 times its actual value; ^^ Coefficient reported at 10^6 times its actual value

$^+$ Based on 1 individual animal only; $^{++}$ Models did not receive support (ΔAICc >7)

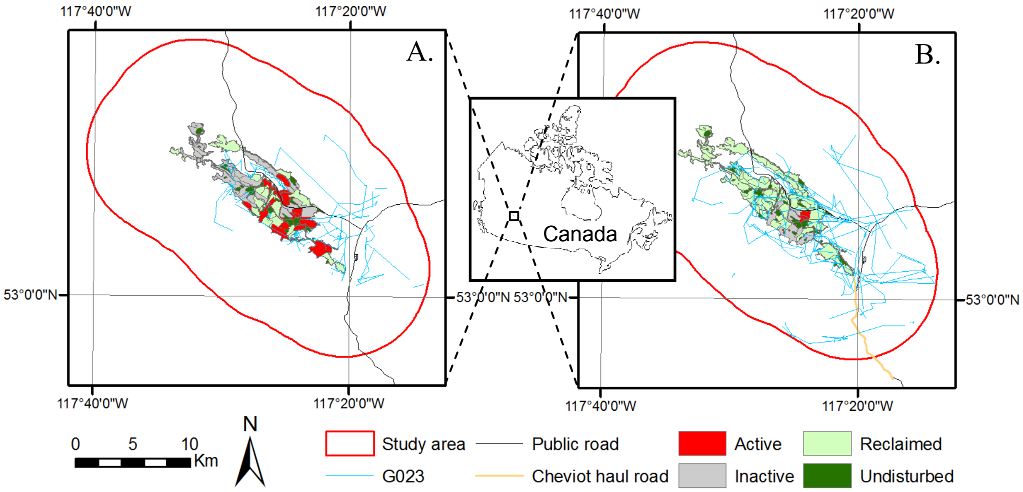

Figure 2.1: Primary study area for grizzly bear movement in west-central Alberta, Canada, delineated by a 7.24 km buffer (red boundary) around two neighbouring open-pit coal mines (Luscar and Gregg River). Two insets are provided for the median years of grizzly bear data availability: during (A-2001) versus after (B-2009) mining to illustrate the dynamic nature of mining activity. The broader study region included the area outside the buffer serving as control for the BACI design, for a total spatial extent of 3,200 km^2. Four-hour path segments of a female grizzly bear with cubs are provided for 2001 and 2009 as an example.

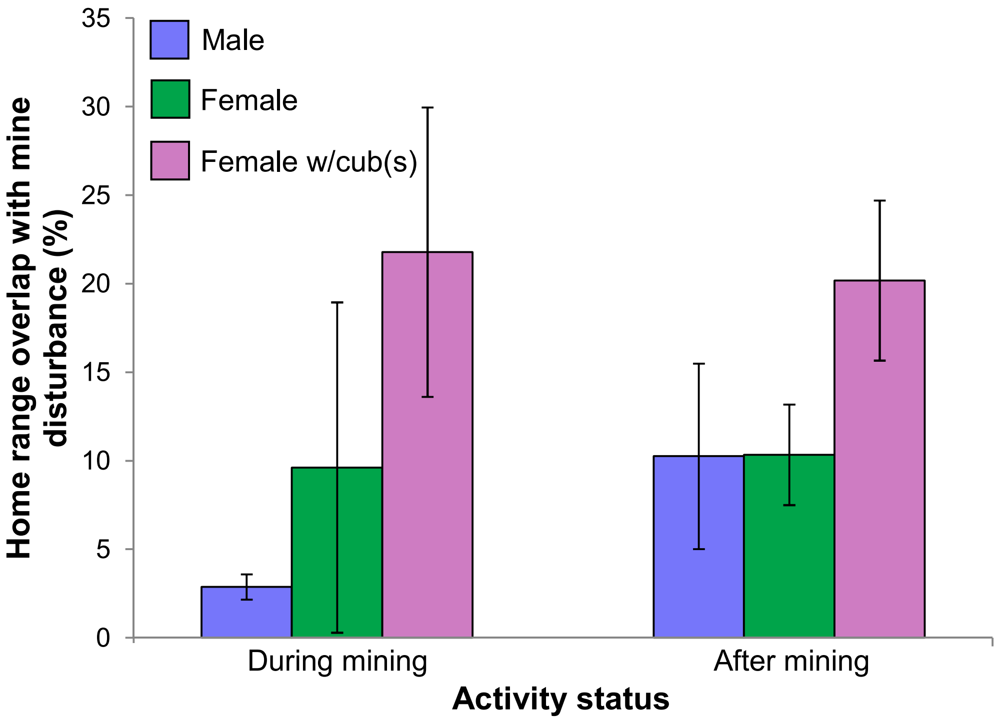

Figure 2.2: Mean grizzly bear annual home range overlap (95% fixed kernel) with Luscar and Gregg River combined mineral disturbance limits, Alberta. Data were collected during (1999-2003) versus after mining (2006 & 2008-2010). Error bars represent ± one standard deviation.

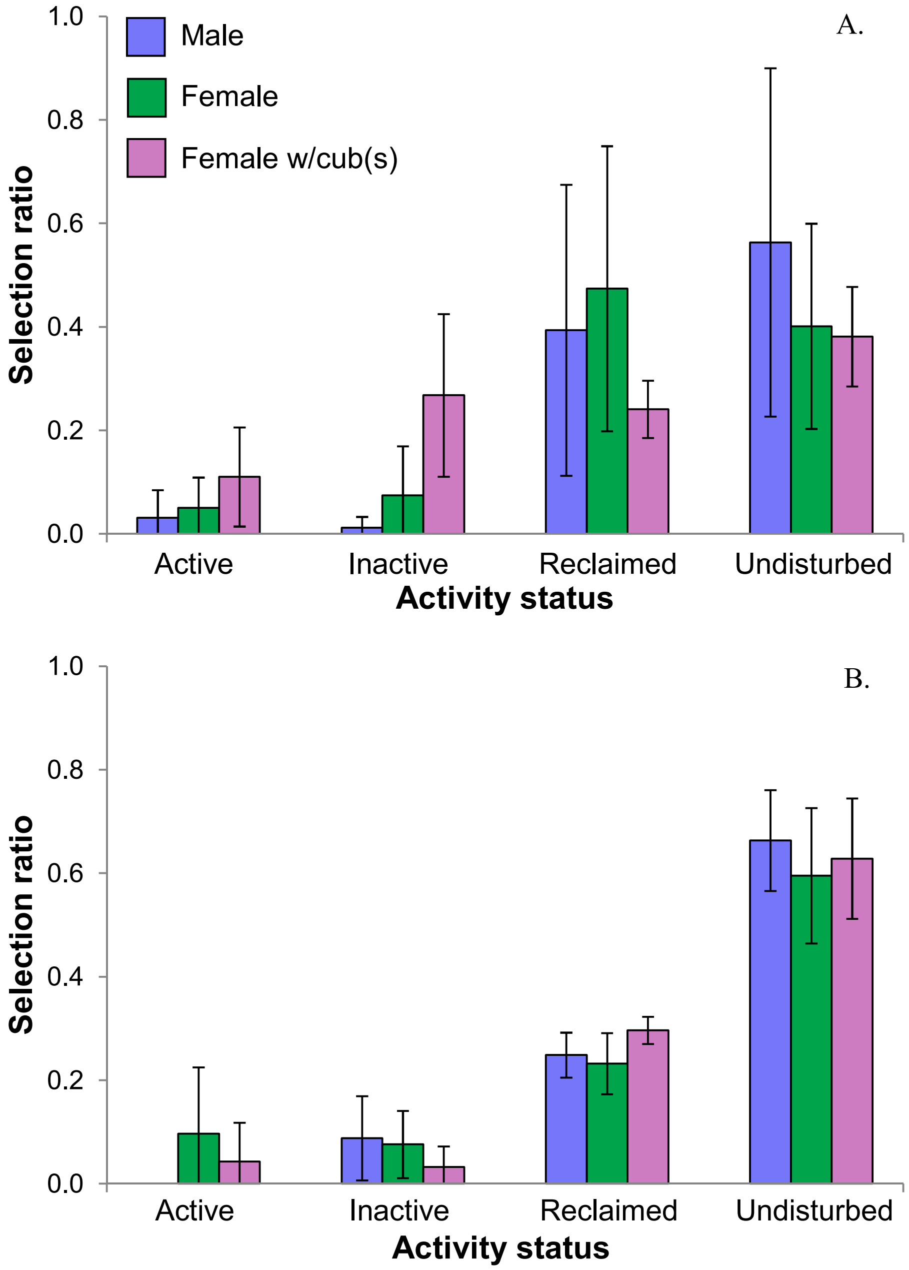

Figure 2.3: Grizzly bear selection of mining status land categories within the merged mineral disturbance limits of Luscar and Gregg River mines, Aberta. Data were acquired (A) during (1999-2003), and (B) after (2006 & 2008-2010) mining. Error bars represent ± one standard deviation.

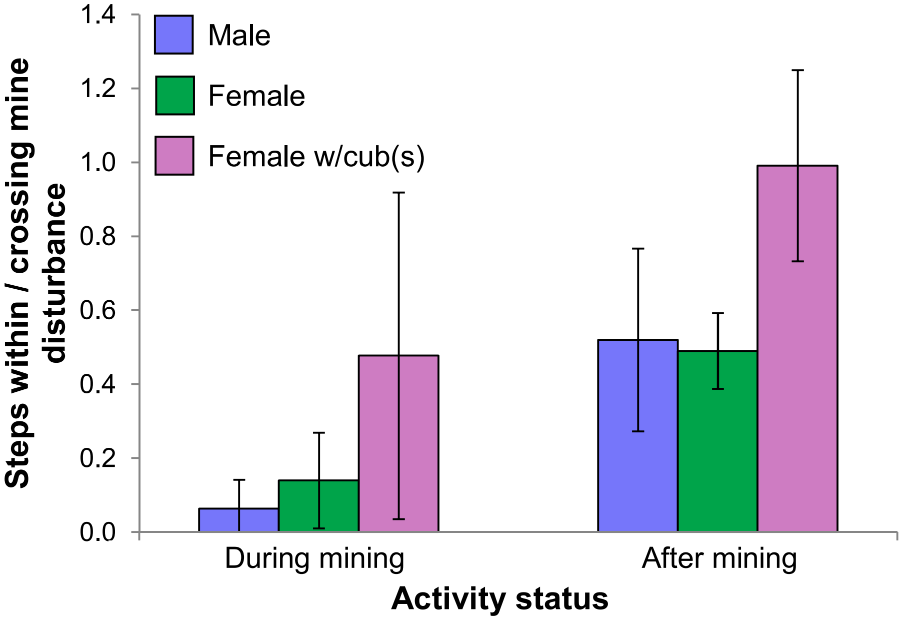

Figure 2.4: Grizzly bear movements in relation to Luscar and Gregg River merged mineral disturbance limits, given as a ratio of steps within disturbance boundary to steps crossing the disturbance limit but starting and/or ending outside the boundary. Error bars represent ± one standard deviation.

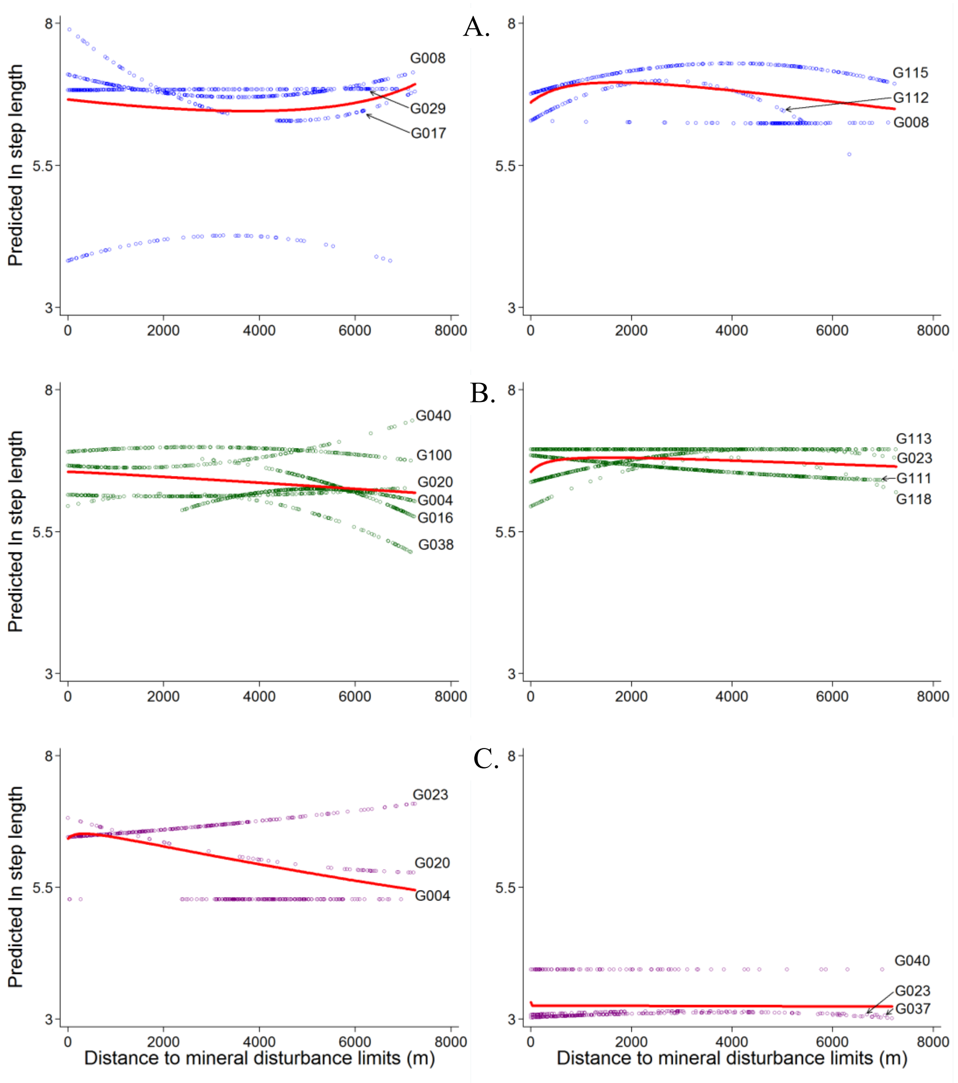

Figure 2.5: Predicted values of ln-transformed grizzly bear steps during (left panels) versus after (right panels) mining based on varying distance to mineral disturbance limits from start location of steps. Red curve represents population-level fit for males (A), females (B), and females with cubs (C).

SUPPLEMENTARY MATERIAL

Grizzly Bear Data

In 2008-2010, I captured and set GPS radiocollars (ATS, Isanti, USA; Followit, Lindesberg, Sweden) on grizzly bears in the broader Yellowhead Ecosystem region, with support from the Foothills Research Institute Grizzly Bear Program (Hinton, Alberta), who also provided data for 1999-2003 and 2006. Twenty-seven adult individuals (>4 years old, based on cementum annuli from a premolar extracted at capture) used the study area during the monitoring period and 19 were included in analyses because of sample size limitations. Analyses included 12 bears monitored during mining ($n_{males} = 5$; $n_{females} = 6$; $n_{females\ with\ cubs} = 5$), and 10 bears monitored after mining ($n_{males} = 4$; $n_{females} = 4$; $n_{females\ with\ cubs} = 3$). Monitoring duration was slightly higher during compared to after mining for males (during: $\text{mean}_{days} = 135$, range = 111−154; after: $\text{mean}_{days} = 110$, range = 34−119), females (during: $\text{mean}_{days} = 167$, range = 121−187; after: $\text{mean}_{days} = 145$, range = 116−176), and females with cubs (during: $\text{mean}_{days} = 154$, range = 121−201; after: $\text{mean}_{days} = 128$, range = 103−156). Some females were accompanied by cubs in some years and single in other years of a specific mining phase. Three bears were monitored both during and after mining.

All capture and handling operations were approved by the University of Alberta and University of Saskatchewan Animal Care and Use Committees. To minimize potential bias related to possible differences in bear response to a specific capture technique, I used a variety of methods including aerial (helicopter darting) and ground capture (culvert traps and minimal leg-hold snaring) (Cattet et al. 2008). GPS fix rate varied across collars, with most of the during active mining relocation fixes acquired at 4-h. Therefore, I rarefied all GPS data to this fix interval and connected relocations with straight lines representing movement steps of bears outside winter denning. This resulted in a series of movement segments representing a sample of the movement path for each bear during each year. Analyses by time of day were precluded because GPS fixes for 1999-2003 were programmed at variable times, but this is not a major shortcoming because disturbance from active mining operations occurs 24-h a day.

Study Design and GIS Data

I defined active mining as vegetation clearing, soil disturbance, overburden blasting, overburden/coal removal and overburden dumping. Available annual land cover layers (30-m grain) were mosaiced with corresponding land cover classification that I performed based on detailed knowledge of the area, coupled with overlaying high resolution orthorectified aerial photos and SPOT imagery (Systeme Pour l'Observation de la Terre/French Earth Observation System) available for 2001, 2004, 2007 and 2010. These corrections to land cover were necessary to reflect the dynamic nature of mined landscapes which incorporate cover types that may receive erroneous spectral reflectance scores in regional scale land cover classification. To make habitat categories more relevant to hypothesized perceived security by bears in terms of landscape openness/visibility, seven land cover categories from the original classification were reclassified to two land cover types including closed (forest) and open (shrub, grassland, and barren land). Edge between closed and open land cover classes was extracted from the rasters and used to calculate Euclidean distance to edge. Terrain ruggedness was derived from a DEM (Digital Elevation Model), using an equation from Nielsen et al. (2004). The equation relates aspect variation and mean slope in a circular 300-m moving window, a size shown to influence grizzly bear occurrence (Theberge et al. 2002, Nielsen et al. 2004). Closed forest (Munro et al. 2006), close proximity to edge (Ordiz et al. 2011) and rugged terrain (Nellemann et al. 2007) were used as surrogates for perceived security by bears. Distance to major public roads and distance to MDL also were calculated, with the latter being a key variable in my assessment of mining effects on bear movements. Lastly, polygons depicting mining activity status were updated every year based on consultation with the mining companies and coded as either active, inactive, reclaimed, or undisturbed (Table 2.1).

Ranging Patterns and Selection of MDLs

I created annual 95% fixed kernel home range polygons for each bear using Hawth's Analysis Tools for ArcGIS (Beyer 2004), clipped polygons by MDL extent and calculated percentage of home range that overlapped the mining area. I then generated random locations at a density of 30 locations/km^2 (Northrup et al. 2012) and intersected bear used locations and random locations with the mining activity status layer for the respective year. Selection ratios for each bear and mining status class were calculated by dividing the number of used locations by the number of available locations (Manly et al. 2002). To avoid the potential influence of large but seldom used 'habitats', selection ratios were standardized to a sum of 1 by dividing the selection ratio for each mining status class by the sum of selection ratios across all 4 status classes.

Movements in Relation to Activity Status within the MDL

For the extent of mine disturbance limits, I investigated grizzly bear step length as a function of mining 'habitat' a step started from. The outcome variable in generalized linear models with Gaussian family error distribution was log transformed step length data, with separate models created for each individual bear. I restricted the analysis to bears with at least 20 steps starting within the MDL. The only covariate employed was the categorical mining activity status at the start location of a step. I verified the assumption of normal distribution of deviance residuals by creating histograms and overlaying a normal distribution on the frequency bins. Robust standard errors were used to account for potential misspecification of the family distribution.

Movements in Relation to the MDL

I separated bear steps into two categories: 1. steps that intersected the MDL having start and end locations outside the MDLs, or either the start/end location outside the MDL; and 2. steps that were entirely within mining boundaries. I created an index of movement by taking the ratio of number of steps entirely within the MDL to steps intersecting the MDL. Counts of steps in the two categories were contrasted during and after mining by performing chi-square tests for each bear reproductive class (male, female, female with cubs).

Movements in Relation to the Cheviot Mine Haul Road

I computed all haul road crossings by intersecting the bear movement paths with a polyline feature representing the haul road location. Haul road construction occurred in 2004 for which no bear movement data were available. Crossings were binned in before (1999-2003) versus during haul road presence and mine traffic (2006 and 2008-2010). To minimize confounding effects related to mining activity within the MDL on bear crossings, analyses were restricted to the haul road section located outside the mine boundaries (10.6 km). I extracted length weighted mean distances to haul road, forest edge, and terrain ruggedness along steps and compared them before versus during haul road activity using two-sample Wilcoxon rank-sum (Mann-Whitney) tests. Because data on haul road crossing by males during the active mining phase were unavailable, I excluded males from analyses. Female data were pooled across reproductive status categories because of small sample sizes. Length weighted means were computed by dividing each movement step into segments that passed through single raster cells. The length of each segment was multiplied by the value of the raster cell, summed across the entire step, and divided by the total step length.

Movements at the Study Area Level

Rather than relying on a statistical model (such as broken-stick approach) to identify cut-offs in empirical step length distributions presumably indicative of bear behaviour, I used radius data from GPS location clusters with known bear activity (Chapter 3) to separate short and long bear movement steps by sex and reproductive status. Short steps are likely associated with concentrated bear activity such as bedding or handling an ungulate carcass, differing from long steps that are more indicative of movement or vegetation consumption. The cut-off in step length was calculated based on the maximum GPS cluster diameter as identified from field visitation of clusters representing bedding and kill events, and differed slightly for males (160 m), females (146 m) and females with cubs (154 m). Selection of clusters for visitation and diameter calculations were based on an algorithm created by Knopff et al. (2009), and modified to incorporate a minimum of 3 GPS locations and 50-m initial seed cluster. Because short steps may be more prone to GPS error (Frair et al. 2005, Jerde and Visscher 2005), and distance to MDL was not a statistically significant covariate for male, female or female with cubs step lengths, I focus hereafter on modeling long movement steps.

The modeling framework followed a two-step approach recommended by Fieberg et al. (2010), which derives population level inferences based on individual level models. Only bears with ≥50 4-h movement steps within the study area extent for any given year were included in statistical analyses. I used generalized linear models with natural log step length as an outcome and a suite of 10 *a priori* selected covariate combinations as predictors, running separate models for each bear of a given reproductive status and mining phase (during versus after). When deemed biologically relevant, squared terms and an interaction were included in candidate models (Table S.1) and all testing estimated robust standard errors. Because I was concerned that bears may be taking longer steps in mountainous areas than in the foothills in relation to topography, making use of ridges or valleys, which may have masked the effects of distance to MDL, for each bear I tested for differences in mean lengths of steps taken exclusively in mountains, foothills, and those that included both mountains and foothills. Following Munro et al. (2006), mountains were defined as elevations >1,700 m, and testing of step length differences was carried out using one-way ANOVAs with log transformed step length as variable of interest. Step lengths for some bears did not differ between mountains, foothills, and mountains and foothills (for steps including both elevation classes), whereas in cases where they did differ, Bonferroni post-hoc analysis showed that steps were actually shortest in the mountains. Given that certain individuals within any reproductive class had steps shorter in the mountains during both phases of mining (during versus after), because I sampled bears that used both mountains and foothills, and because terrain ruggedness was included as a covariate in the candidate model set, I consider any topographical bias minimal.

I ranked models for each individual using AICc and because no model received substantial support (w_{AICc} <0.9), I used model averaging to obtain coefficient estimates within each individual (Symonds & Moussalli 2011). Averaging was carried out only for models that received substantial or some support (ΔAICc ≤7) (Grueber et al. 2010) using the equation

$$\beta_{kj} = \sum_{i=1}^{R} w_i \beta_i$$

where β_{kj} is the estimate of coefficient k for individual j, across all i models that received support in model ranking, with $i = \overline{1, R}$. I then averaged regression coefficients separately across males, females, and females with cubs respectively for during versus after mining, using the following equation recommended by Marzluff et al. (2004).

$$\overline{\beta_k} = \frac{1}{n} \sum_{j=1}^{n} \beta_{kj}$$

Next, I estimated the variance of each model coefficient using the variation between monitored grizzly bears and the equation

$$\mathrm{Var}\left(\overline{\beta_k}\right) = \frac{1}{n-1} \sum_{j=1}^{n} \left(\beta_{kj} - \overline{\beta_k}\right)^2$$

Finally, I computed standard population-level 90% confidence intervals separately for each reproductive status and mining phase, based on variance calculated according to equation above.

BACI Calculations for Movements at the Study Area Level

A control area where grizzly bear movements were monitored was set beyond a 7.24 km buffer around the MDL. The buffer radius for the control was delineated based on the 95th percentile 4-h step length of bears monitored. I used standard artithmetic formulas to calculate the normalized (log-transformed) weighted mean difference and standard deviation in step lengths between treatment and control; i.e., between steps potentially influenced by mining (within the buffer) and steps in the control area (outside the buffer). Weights were bear-specific and obtained by dividing the number of steps for an individual by the total number of steps recorded for that specific reproductive class (male, female, or female with cubs). Separate calculations were performed for each reproductive class, mining phase (during, after) and control (control 1: during, control 2: after).

To assess the effect of mine 'manipulation' on bear movements, I used a *t*-test to compare the normalized mean differences in step length during versus after Impact/mine closure. The pooled estimate of the standard deviation (s_p) was

$$s_p = \sqrt{\frac{(n_1 - 1){s_1}^2 + (n_2 - 1){s_2}^2}{n_1 + n_2 - 2}}$$

where n_1 is the sample size (number of steps) and s_1 is the standard deviation of step length during mining, n_2 is the sample size and s_2 is the standard deviation after mining. The *t*-statistic to compare the means was

$$t = \frac{(\overline{x_1} - \overline{x_2})}{s_p \times \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}}$$

where $\overline{x_1}$ is the mean difference (treated − control) during mining, and $\overline{x_2}$ is the mean difference (treated − control) after mining. The calculated *t*-statistic value was compared to the critical value for significance at $\alpha = 0.05$ with $n_1 + n_2 - 2$ degrees of freedom.

Literature Cited

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. [online] URL: http://www.spatialecology.com/htools

Cattet, M., J. Boulanger, G. Stenhouse, R. A. Powell, and M. L. Reynolds-Hogland. 2008. An evaluation of long-term capture effects in ursids: Implications for wildlife welfare and research. Journal of Mammalogy **89**:973-990.

Fieberg J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2153-2312.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology **20**:273-287.

Grueber, C. E., S. Nakagawa, R. J. Lewis, and I.G. Jamieson. 2010. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology **24**:699-711.

Jerde, C. L., and D. R. Visscher. 2005. GPS measurement error influences on movement model parametrization. Ecological Applications **15**:806-810.

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.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dodrecht, The Netherlands.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: Forest fragments and Steller's Jays. Ecology **85**:1411-1427.

Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy **87**: 1112-1121.

Nellemann, C., O.-G. Stoen, J. Kindberg, J. E. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. P. Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an an expanding brown bear population in relation to age, recreational resorts and human settlements. Biological Conservation **138**:157-165.

Nielsen, S. E., S. Herrero, M. S. Boyce, B. Benn, R. D. Mace, M. L. Gibeau, and S. Jevons. 2004. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies Ecosystem of Canada. Biological Conservation **120**:101-113.

Northrup, J. M., J. Pitt, T. B. Muhly, G. B. Stenhouse, M. Musiani, and M. S. Boyce. 2012. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. Journal of Applied Ecology **49**:1159-1167.

Ordiz, A., O.-G. Stoen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia **166**:59-67.

Symonds, M. R. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology **65**:13-21.

Theberge, J. C. 2002. Scale-dependent selection of resource characteristics and landscape pattern by female grizzly bears in the eastern slopes of the Canadian Rocky Mountains. Ph.D. dissertation, University of Calgary, Calgary, AB, Canada.

Table S.1: Candidate model set for habitat security features hypothesized to influence grizzly bear step length within the primary study area extent (7.24 km buffer around Luscar and Gregg River mine disturbances, Alberta). Numbers under reproductive status heading represent percentages of the respective model type that were included in model averaging across individual bears.

Model	**Model structure**	K_i	**Male**		**Female**		**Female w/cubs**	
			During	After	During	After	During	After
1	TRI + TRI^2 + Cov2 + Dedge + Dedge^2 + Dmdl + Dmdl^2 + Droad + Droad^2 + Cov2 × Dmdl	9	7.69	6.25	14.29	16.67	7.69	0
2	TRI + TRI^2 + Cov2 + Dedge + Dedge^2 + Dmdl + Dmdl^2	8	7.69	12.5	14.29	16.67	7.69	0
3	TRI + TRI^2 + Cov2 + Dedge + Dedge^2 + Droad + Droad^2	8	15.38	12.5	11.43	8.33	7.69	0
4	TRI + TRI^2 + Cov2 + Dmdl + Dmdl^2 + Cov2 × Dmdl	7	7.69	6.25	14.29	16.67	15.38	25
5	Cov2 + Dedge + Dedge^2 + Dmdl + Dmdl^2 + Cov2 × Dmdl	7	7.69	6.25	5.71	0	0	0
6	Cov2 + Dmdl + Dmdl^2 + Cov2 × Dmdl	5	23.08	18.75	11.43	16.67	7.69	0
7	Cov2 + Droad + Droad^2	4	7.69	12.5	5.71	0	15.38	0
8	Dmdl + Dmdl^2	3	15.38	12.5	14.29	25	7.69	25
9	Droad + Droad^2	3	7.69	6.25	5.71	0	23.08	50
10	Cov2	2	0	6.25	2.86	0	7.69	0

Table S.2: Predicted individual-level grizzly bear step length as a function of mining status at Luscar and Gregg River open-pit coal mines, Alberta, Canada (1999-2003, 2006; 2008-2010 data). GLM-based predictions included 'long' steps not associated with ungulate consumption or bedding behaviours as identified from GPS cluster investigations (step length by reproductive status [RS]: males ≥160 m, females ≥146 m, female with cubs ≥154 m). Significant terms are given in bold. Steps starting in the undisturbed mining category were withheld as base category. No reporting of coefficients corresponds to no steps starting in the respective mine activity class.

Bear ID	**Sex**	**RS**	**Intercept**			**Active**			**Inactive**			**Reclaimed**		
			β_i	90% CI		β_i	90% CI		β_i	90% CI		β_i	90% CI	
				Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
During mining														
G020	F	Single	**4.728**	**3.524**	**5.932**	**2.261**	**0.741**	**3.781**	1.098	−0.214	2.410	**1.340**	**0.081**	**2.598**
G040	F	Single	**6.479**	**5.817**	**7.140**	−0.043	−1.306	1.220	−0.385	−1.215	0.445	0.057	−0.894	1.009
G023	F	COY	**6.171**	**5.675**	**6.666**	−0.327	−0.974	0.321	0.257	−0.344	0.857	−0.675	−1.451	0.101
G040	F	COY	**5.505**	**4.992**	**6.017**	−0.268	−1.077	0.540	**1.41**	**0.759**	**2.062**	**0.806**	**0.192**	**1.421**
G029	M		**5.236**	**4.619**	**5.853**	**1.841**	**0.397**	**3.285**	**3.061**	**2.155**	**3.966**	**0.849**	**0.179**	**1.518**
After mining														
G023	F	Single	**5.149**	**4.597**	**5.70**	1.005	−0.631	2.641	**1.951**	**1.128**	**2.774**	0.559	−0.045	1.162
G111	F	Single	**5.778**	**5.118**	**6.438**	**2.086**	**1.426**	**2.746**	0.864	−0.501	2.229	0.533	−0.193	1.259
G113	F	Single	**5.059**	**4.542**	**5.576**	**2.188**	**1.569**	**2.807**	0.03	−1.341	1.402	**1.515**	**0.91**	**2.119**
G118	F	Single	**5.867**	**5.259**	**6.475**							0.351	−0.303	1.005
G023	F	Yearling	**5.649**	**5.247**	**6.052**				**0.597**	**0.194**	**0.999**	0.449	−0.017	0.915
G040	F	Yearling	**5.553**	**5.072**	**6.034**	**−2.529**	**−4.495**	**−0.563**	**1.036**	**0.080**	**1.991**	**0.623**	**0.071**	**1.174**
G037	F	2-Yr old	**5.278**	**4.942**	**5.613**							**0.512**	**0.135**	**0.889**
G112	M	Male	**6.373**	**5.938**	**6.808**				0.658	−0.030	1.319	−0.43	−1.004	0.144
G115	M	Male	**5.754**	**5.167**	**6.340**				**3.163**	**2.577**	**3.749**	0.267	−0.366	0.899

CHAPTER 3

PREDICTING COMPLEX BEHAVIOUR FROM GPS RADIOCOLLAR CLUSTER DATA

ABSTRACT

Advancements in GPS radiotelemetry technologies allow collection of large amounts of data for a variety of animal species including those for which direct observations are typically not feasible. Predicting behaviour from telemetry data is possible but telemetry fix rate can influence inferences and animal behaviour itself can affect fix success. I apply multinomial regression models to grizzly bear (*Ursus arctos*) GPS radiocollar cluster data with known behavioural states collected from bears (*n* = 10) in west-central Alberta, Canada, with the purpose of behavioural prediction. Models including cluster parameters, habitat characteristics or combination of both performed differently depending on target behaviour. Cluster parameters provided accurate ungulate kill predictions from the GPS dataset without the need for site-level information. Habitat characteristics at cluster locations were sufficient to identify bear bedding sites, whereas sites with more complex behaviours required both cluster parameters and habitat characteristics. The method could not reliably predict vegetation-feeding by bears probably because this activity is shorter than the time required for cluster formation. Infrequent fix rates underestimated all behaviours, with ungulate kill sites least sensitive to fix rate variability. Behaviour influenced fix success, with highest fix acquisition occurring when bears fed on vegetation. Placing predictions into a conservation context I show behavioural variability for grizzly bears in a landscape with complex human-activity patterns on reclaimed open-pit coal mines, foothill and mountain regions. While studies on animal behaviour are facilitated by direct observation, I demonstrate the use of technology to discern complex animal behaviour even in the absence of visual monitoring.

INTRODUCTION

Patterns of animal distribution in space and time are a product of the underlying process of animal movement (Turchin 1998, Mueller and Fagan 2008, Nathan et al. 2008). Identifying behavioural states along an animal's movement path is straightforward when visual observation of a focal animal is possible (Gillingham and Klein 1992, Bates and Byrne 2009, Hayward et al. 2009). Directly observing an individual to record its behaviour is a common and effective method for investigating animal behaviour, and the least prone to errors of assigning true behavioural state (Loettker et al. 2009, Shamoun-Baranes et al. 2012).

Observing the behaviour of rare or cryptic animals that are wide ranging and/or live in difficult study environments presents major challenges to researchers. Rare species are difficult to locate often resulting in small sample sizes (Caro 2007) or at worst in research program failure. For study animals that pose threats to researcher safety, such as large terrestrial mammals, investigating behaviour via direct observation adds another level of difficulty. Yet an integrative approach that combines behavioural ecology and conservation biology can promote understanding of behavioural processes that determine patterns of interest to conservation decisions. Although the benefits of such an approach are clear (Lima and Zollner 1996, Blumstein and Fernandez-Juricic 2004, Caro 2007), bridging the gap between the two disciplines has so far largely failed (Caro and Sherman 2011).

Considerable recent advancements in GPS radiocollar technologies allow tracking of animals for long sampling periods, providing large datasets of geo-referenced locations at time intervals programmed by the researcher (Cagnacci et al. 2010). Upon direct or remote data retrieval from the radiocollar, the GPS locations can be used to investigate habitat selection (Hebblewhite and Haydon 2010), spatiotemporal movements (Nathan et al. 2008), or habitat influences on animal movement (Schick et al. 2008). By setting the GPS acquisition schedule at regular time intervals radiocollars can collect data that fit the familiar focal sampling with instantaneous recording protocol used in animal behaviour studies (Martin and Bateson 2007). Despite this opportunity, few studies have successfuly estimated mammalian behavioural states from GPS radiocollar data. To predict movement, some studies have decomposed an individual's movement trajectory on the landscape into a broad set of movement bouts based on rates of movement (Johnson et al. 2002). Others have inferred behavioural states based on time required for an animal to first move out of a circle centred on a location along the path (Frair et al. 2005), or total time spent in the vicinity of a location (Barraquand and Benhamou 2008). Patterns of animal space and behaviour also can be investigated using autocorrelation analysis (Wittemyer et al. 2008, Boyce et al. 2010) or generalized additive models for either net squared displacement (Fryxell et al. 2008) or step length (Ciuti et al. 2012). Biotic and abiotic influences along the movement path also have been researched (Fortin et al. 2005), sometimes by incorporating a hidden behavioural state in the analytical procedure (Forester et al. 2007). All the above studies focused on large herbivores, likely reflecting greater movement data availability for ungulates compared to carnivores (however, see Dickson et al. 2005, Roever et al. 2010, Byrne and Chamberlain 2012).

In carnivore studies in which authors attempt to derive behaviour from GPS relocation data, the main goal has often been to identify GPS location clusters indicative of predation events (Merrill et al. 2010). Clusters form when an animal spends a certain amount of time within a site of a given radius, where time and radius are specified by the researcher and should be tailored to the behaviour of the study species and field conditions. For example, a large kill might necessitate a longer time to consume and can result in multiple smaller clusters for the same carcass (Tambling et al. 2012). Less frequent fix rates might minimize the problem of multiple clusters for the same kill, but could result in decreased detection of small carcasses, which likely require shorter consumption time. Regardless of fix rate, if the predator is guarding the prey and the carcass is not moved, the cluster will likely have a small radius. Once clusters have been identified, most authors use logistic regression with a binomial response variable to model kill presence/absence at location clusters based on cluster and/or habitat characteristics (e.g., Webb et al. 2008, Knopff et al. 2009, Tambling et al. 2010, Pitman et al. 2012).

Early attempts to identify location clusters included assigning circles of given radii around carnivore GPS locations (Sand et al. 2005) and using software originally conceived to identify epidemiological clusters (Webb et al. 2008). The publication of a cluster identification algorithm to detect cougar (*Puma concolor*) kill clusters (Knopff et al. 2009), which is easily modifiable to address individual study aims and biology of other species, represented a breakthrough for animal behaviour researchers interested in identifying carnivore kills from GPS radiocollar data. However, the influence of fix success can be important for studies where GPS receivers have poor acquisition, potentially resulting in misinterpretations of biological signals in the data (Frair et al. 2010, Mattisson et al. 2010). In an attempt to account for poor fix success, some researchers have positioned GPS radiocollars at stationary locations in different habitats (Graves and Waller 2006, Heard et al. 2008), applying the resulting corrections to radiocollar data from monitored animals. Nonetheless, certain animal behaviours could affect fix success (Mattisson et al. 2010) and no study has assessed fix success based on GPS fixes from mobile animals, in conjunction with indisputable knowledge of animal behaviour from field visitation (Frair et al. 2010).

I extend the binary logistic regression framework typically applied in carnivore studies to include a multinomial response variable that reflects the ecology of facultative diets. This approach enables identification of multiple behavioural states and is readily applicable to facultative carnivores, as well as obligate carnivores where the goal is to identify behavioural states that are not restricted to kill consumption. Building on the Knopff et al. (2009) cluster algorithm, I present an application of the multinomial method to the study of a facultative carnivore (grizzly bear [*Ursus arctos*]) from a threatened population at the south-eastern edge of this species' range in Canada. I discuss the findings on bear behaviour in relation to human activity and habitat characteristics. I vary the fix rate to estimate its effect on detecting different behavioural states, and test whether behaviour affects fix success in specific habitat types, again using grizzly bears as a focal study species.

METHODS

Study Area

I carried out the study in a 3,200 km^2 area located in west-central Alberta, Canada (approximate central coordinates 53°05' N 117°25' W) (Figure 3.1). The area is situated along an east to west increasing altitudinal gradient incorporating foothills and eastern slopes of the Rocky Mountains (elevation; mean ± SD, 1980 ± 613 m). Boreal forest is the dominant land cover being composed of lodgepole pine (*Pinus contorta*), white (*Picea glauca*) and black spruce (*P. mariana*), balsam fir (*Abies balsamea*) and subalpine fir (*A. lasiocarpa*). Mixed and to a smaller extent deciduous forest occur primarily in the eastern section of the study area and are dominated by balsam polar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*). Shrub cover is present above the tree line and along river valleys and dominated by willow (*Salix* spp.), dwarf birch (*Betula* spp.) and alder (*Alnus* spp.). Grasslands and barren (non-vegetated) land are present on two reclaimed open-pit coal mines with limited and restricted motorized and non-motorized human access. The mountainous region includes protected areas and generally has lower levels and fewer types of human influences compared to the foothills region. In the latter, oil and gas activities, logging, motorized recreation and hunting occur.

Study Animals

The grizzly bears I sampled persist at one of the lowest densities recorded for the Alberta threatened grizzly bear population (Boulanger et al. 2005). In 2008-2010, with assistance from the Foothills Research Institute Grizzly Bear

Program (Hinton, Alberta), I captured and deployed remotely downloadable GPS radiocollars (Telus UHF; Followit, Lindesberg, Sweden) on twelve adult grizzly bears. I attempted to sample the bear population randomly in the foothills (elevation <1,700 m), mountains (≥1,700 m) and on reclaimed mines, using helicopter darting and ground capture (culvert traps and limited leg-hold snaring) (Cattet et al. 2008). Two large male bears dropped their collars within a month from capture and were excluded from analyses. I monitored the remaining ten bears ($n_{males} = 4$; $n_{females} = 5$; $n_{females\ with\ cubs} = 2$) for a total of 67.1 bear-months (6.7 ± 4.1 months per bear). One female had cubs in 2009 and was single in 2010. Radiocollars were set to acquire a location hourly during March 15 - December 1, when bears were primarily outside their winter dens. This fix rate was a compromise between sufficiently detailed data for tracking behaviours and collar battery life. To acquire data for field visitation of sites used by bears each month I approached every bear on foot or via fixed-wing aircraft or helicopter and triggered its radiocollar to send GPS data remotely via VHF transmission.

GPS Cluster Visitation

Initial attempts to assess bear behaviour at unique GPS relocations typically resulted in sites with unknown behaviour, therefore I focused visitation and analyses on GPS relocation clusters. I sampled clusters for field recording of bear behaviour by running the Python algorithm originally designed for cougar kill site identification (Knopff et al. 2009), which I modified to include 50-m seed cluster radius because I considered it was not logistically possible to effectively search radii >50 m (i.e. >7,850 m^2). Because of logistical limitations, for each bear during each month I attempted to visit the largest four clusters and randomly picked other clusters, provided they had ≥3 telemetry relocations within a temporal window of 6 days.

At the cluster centroid, crews searched for evidence of bear behaviour on a 50-m radius using protocols adapted from Munro et al. (2006) who studied the same bear population. A 20×20-m square plot (oriented north to south) was centred on the most time consuming bear activity, where ungulate carcass feeding was designated as the lengthiest activity, followed by bedding, and vegetation feeding. All bear behaviour sign within the plot was recorded. Sites where bears had fed on an animal included hair and skeletal remains, displaced rocks and logs when bears looked for small mammals, or split logs and disturbed ant hills when bears searched for ants. Vegetation feeding sites contained digs for *Hedysarum* spp. roots, disturbed berry shrubs, and/or grazed herbaceous vegetation. In assigning bear behaviour I considered age of sign such as algal growth on carcass bones, plant shoot growth inside digs and beds, or greenness of grazed vegetation. When bear scats were present, these were checked for presence of hair, bone fragments, ants, root material, berries, or herbaceous vegetation possibly indicative of site behaviour. Terrain variables (slope, aspect, elevation) were recorded within the plot. Biotic variables recorded included land cover (classified as barren/herbaceous, shrub, conifer forest, or mixed conifer-deciduous forest), vertical canopy (with a spherical densiometer) and stand basal area (using a 2-m prism).

Grizzly Bear Behaviour Predictions

I modeled bear behaviour assigned during GPS cluster field visitation using STATA v.11.2 (StataCorp, College Station, Texas). Behaviour was coded as: 1. vegetation feeding (root digging, grazing or berry feeding); 2. bedding; 3. vegetation feeding with bedding; 4. carcass feeding with or without bedding. Although I initially attempted to create separate models for each bear social group (males, females, females with cubs) I ran into convergence problems because of insufficient sample sizes and all analyses reported herein are for data pooled across social groups.

I applied the framework detailed in Zuur et al. (2009) to decide whether to use a fixed-effects modeling approach, or more complex mixed models incorporating fixed effects and a random intercept for bear unique identity (*bear_id*). This method uses a likelihood ratio test to compare the global fixed effects and global mixed effects models (incorporating all *a priori* relevant predictor variables). Fixed and mixed effects models were implemented using the Generalized Linear Latent and Mixed Models framework (STATA's gllamm) with multinomial logistic regression (mlogit) link. The mixed effects model did not show any performance improvement over the fixed effects model (LR $\chi^2 = 0.00$, $df = 1$, $P = 1.00$), therefore I used multinomial regression in a fixed effects framework for all analyses.

I formulated *a priori* hypotheses on model variables that might influence model fit and grouped them into three categories: behaviour (based on location cluster features), habitat (only habitat features) and behaviour and habitat (based on both cluster and habitat characteristics). Behavioural variables intrinsic to the cluster were: number of locations in cluster, divided by the proportion of successful fixes during cluster persistence, to account for varying fix success (*cl_points*); a categorical variable for whether cluster spanned 24-h (1) or more (0) (*cl_24h*); cluster fidelity defined as a ratio of number of locations at cluster divided by number of locations away (>50 m) from the cluster during the cluster duration (*cl_fidelity*); the average distance from each cluster location to the centroid of the cluster (*cl_avg_dist*); and cluster radius defined as the maximum distance from the centroid to the outermost point in the cluster (*cl_radius*). Habitat variables included in candidate models were: land cover class (*hab*), including barren and herbaceous (1), shrub (2), conifer forest (3) and mixed forest (4); slope in percentage (*slope_p*); and site severity index (Nielsen and Haney 1998) (*ssi*):

$$ssi = \sin(aspect + 225) \times \frac{\%slope}{45}$$

For each model category I also tested the potential influences on bear behaviour caused by season (*season*), time of day (*time_day*) and location (*land_loc*) on the landscape. Seasonal classification cut-offs followed Nielsen et al. (2004) and included hypophagia (den emergence to June 14) (1), early hyperphagia (June 15 to August 7) (2) and late hyperphagia (August 8 to den entrance) (3). Time of day was computed based on the first location within the cluster, and classified as diurnal (sunrise to sunset) (1), crepuscular (morning twilight to sunrise and sunset to evening twilight) (2) or nocturnal (evening twilight to morning twilight) (3). Sunrise, sunset and civil twilight tables (http://www.cmpsolv.com/los/sunset.html, accessed October 17, 2011) corresponded to study area location. Finally, I accounted for cluster location based on a combination of elevation and land use, distinguishing between reclaimed open-pit mines regardless of elevation (1), foothills (<1700 m) (2) and mountains (≥1700 m) (3). Bear diet composition and resting-site selection have differences between these three locations (Chapters 4 and 6), which also have varying human activity (see Study area section).

I tested for correlations between predictor variables and excluded highly correlated variable combinations ($|r| > 0.6$) from all candidate models. Cluster radius was correlated with cluster average distance therefore I tested two sets of candidate models, one for each of these two variables. The best models based on log likelihood were the ones incorporating cluster average distance, therefore the respective model set was withheld and the cluster radius variable was dropped. All models were fitted by specifying the robust standard error to estimate asymptotically correct variances. For each category, I ranked models based on ΔAICc and model weights derived from Akaike's Information Criterion for small sample sizes. The top three models (four if the weights for two models were identical) from each category were then included in a second and similar model selection procedure which ranked competing behaviour, habitat and behaviour + habitat models. I checked for potential collinearity between predictor variables for all top models using variance inflation factors (VIF) and calculated percent deviance explained for each top model as a measure of model fit.

I assessed model fit with Wald chi-square tests and plotted Pregibon leverage values against predicted probabilities of specific behaviours to detect potential observations that disproportionately influenced fit. I used the probability output from the top multinomial regression model to assign type of behaviour at a cluster. The multinomial output with four categories for the response variable included four probabilities, one for each behaviour. I used a cut-off that equaled the largest of the four predicted probability values for assigning behaviour (Maarten L. Buis, University of Tuebingen, pers. comm. on STATA list). I assessed the predictive capacity of the top models for each of the three sets (behaviour, habitat, behaviour and habitat) by using 4-fold cross validation, based on Huberty (1994), with approximating a 75/25 model training-to-testing ratio.

Influence of Fix Rate on Behavioural Inferences

In most GPS radiocollars relocation frequency (fix rate) has to be pre-programmed by the user. To assess how fix rate influences outcome of the cluster algorithm, and hence behavioural inferences, I re-ran the algorithm maintaining constraints constant but varying fix rate as follows: 1-h (baseline), 2-h, 4-h, 6-h, 8-h, and 12-h. Using behavioural data based on model predictions, I calculated proportion of different behaviours detected by the cluster algorithm at different fix rates. I assumed that the algorithm correctly identified behaviour if the cluster centroid was located within 50 m of the actual behaviour location. I inspected the confidence limits around the proportion of behaviours identified by the algorithm for each fix rate to assess the rate necessary to identify specific behaviours.

Influence of Behaviour on Fix Success

The radiocollars used in this study had excellent but not 100% fix success (mean ± SD, 93 ± 11% for clusters visited in the field). I took advantage of behaviour data collected during field visitation to test the hypothesis that behaviour of the radiocollared animal influences fix success. I used generalized linear models (STATA's glm) where the response variable (% fix success) was rescaled to proportion fix success (values in the [0,1] range) to allow application of models in the binomial family with logit link. Proportion successful fixes for relocation clusters was calculated as:

$$Fix\ success = \frac{cl\_fixes + cl\_away}{cl\_theoretical}$$

Where *cl_fixes* are fixes successfully acquired at the cluster; *cl_away* are fixes acquired between the first and last fix in the cluster, but which were not at the cluster; and *cl_theoretical* represents the total number of fixes between the first and last fix number in the cluster. I estimated univariate models with behaviour as independent variable, separately for each habitat, for a total of four models. The behavioural and habitat variables were categorical and had the same classes as described in the section on predicting bear behaviour. To obtain conservative estimates by making analyses relevant to the scale at which I had recorded bear behaviour in the field, I restricted the data to clusters with radii <15 m and with 0 relocations away from the cluster. Robust standard errors were used to account for potential misspecification of the distribution family. For each model I computed VIF, calculated percent deviance, and assessed fit by inspecting deviance residuals for potential outliers or influential observations. Finally, I correlated predicted values to observed values of the dependent variable, considering high correlations indicative of good predictive power (Zheng and Agresti 2000).

Grizzly Bear Behaviour in a Multiple-use Landscape

I used predictions from the most accurate of the three top models for each set (behaviour at cluster, habitat at cluster, behaviour and habitat at cluster) to calculate frequency of occurrence of the specific behaviours (vegetation feeding, bedding, vegetation feeding with bedding, carcass feeding) by land designation. For each behavioural state I calculated differences between observed and expected frequencies of occurrence between land designations using chi-square analyses, for a total of four tests. I set expected frequencies to be equal among land designations and applied a correction factor to each observed frequency value to account for unbalanced sampling design between land designations. For example, if more predicted clusters across all behaviours occurred in the mountains than in the foothills or reclaimed mines, then I calculated correction factors by dividing the total number number of clusters in the mountains by the total number of clusters in the foothills, and dividing the total number of clusters in the mountains by the total number of clusters on reclaimed mines. The results of these two divisions would then be multiplied by the number of clusters for the predicted behaviour of interest for foothills and reclaimed mines respectively, whereas the number of predicted clusters for the respective behaviour in the mountains remained unchanged.

RESULTS

During the 3-year study I visited 550 grizzly bear GPS location clusters. Based on initial experiences of surprising bears at large ungulate kill clusters even three weeks after cluster initiation, and logistical constraints of study area accessibility, field visitation occurred within a safe time interval lag following the first fix in the cluster (40.6 ± 15.5 days). I found evidence of bear behaviour on average 10.6 ± 18.3 m away from the geometric centre of the cluster. Rarely detected or unknown bear behaviours as described below occurred at 49 clusters (8.9%), which were excluded from analyses to minimize concerns over predictive ability. Nine excluded clusters had unknown bear activity and 34 clusters had rodent digging, ant consumption or tree rubbing. I also eliminated 4 clusters with complex behaviour including bedding, carcass, and vegetation feeding, and 2 clusters on active mine sites. The final dataset of 501 field validated clusters (mean ± SD, 50.1 ± 34.0 clusters/bear) included four behavioural states: vegetation feeding (n = 53), bedding (n = 232), vegetation feeding and bedding (n = 83), and carcass with or without bedding (n = 133). Most clusters visited were in the foothills ($n_{clusters}$ = 247, 49.3%) and mountains ($n_{clusters}$ = 179, 35.7%). Only 75 clusters (15%) were visited on reclaimed mines, reflecting bear spatial distribution on the multiple-use landscape.

Grizzly Bear Behaviour Predictions

Of the total of 43 models considered (behaviour at cluster, n_{models} = 13; habitat at cluster, n_{models} = 11; behaviour and habitat at cluster, n_{models} = 19), only the top model for each *a priori* defined set of hypotheses received support, with all other models receiving no support (ΔAICc>10) (Tables S.1-S.3 in Supplementary material). The top three models were global models that included 7 predictor variables (behaviour set, habitat set), and 11 variables (behaviour and habitat set). Each of these top models had an AICc weight of 1 within its respective set, explaining up to 35.7% of deviance (Table 3.1). Although the top model from the behaviour and habitat set explained the highest deviance, it was not the best at predicting the field observed behavioural composition across all four behavioural states considered (Table 3.2). Based on 0.80 mean predicted proportion of true composition and low variability between partitioned data sets (SD = 0.12), the behaviour and habitat model was the best for predicting vegetation feeding with bedding. The habitat model was the best at predicting bedding alone (0.75 ± 0.23), and the behaviour model was best at predicting ungulate consumption (0.48 ± 0.01). Vegetation feeding was poorly predicted by all models, with the habitat model being slightly better than the other models (0.18 ± 0.20).

I summarize strong patterns of behavioural state occurrence as predicted by the top three models, with both strong and weak patterns reported in Tables 3.3-3.5. According to model predictions, clusters corresponded primarily to feeding on vegetation and bedding, or bedding alone, with fewer clusters representing vegetation feeding or ungulate consumption, respectively. Number of locations at cluster was a strong universal predictor across all behaviours. Vegetation feeding was less likely to occur compared to bedding if clusters included a large number of locations, whereas vegetation feeding with bedding, and carcass feeding were more likely to occur when clusters had many locations. Vegetation feeding clusters averaged 5 ± 2.8 locations, bedding clusters 7 ± 4.5 locations, vegetation feeding and bedding had 9 ± 7.9, whereas ungulate consumption had 26 ± 26.9. Bears were more likely to show infidelity to carcass sites compared to bedding. Vegetation feeding clusters had higher cluster average distances (14.9 ± 6.8 m) than bedding clusters (12.2 ± 6.1 m). Based on the behaviour model estimation, cluster average distance also was lower than the corresponding vegetation feeding measure when bears fed on a carcass (13 ± 5.7 m).

Vegetation feeding and vegetation feeding with bedding clusters were less likely in conifer forest compared to bedding. The habitat at cluster model predicted that ungulate consumption clusters were more likely as slope decreased. Based on all three top models, clusters occurring in the fall were less likely to include vegetation feeding and ungulate consumption behaviours than those in spring. According to the two models that included behaviour, clusters occurring in summer were less likely to represent vegetation feeding than spring clusters. In addition, the habitat model predicted carcass feeding clusters to occur less frequently in summer than in spring. Based on the behaviour model, clusters representing vegetation feeding with bedding were predicted to occur more when the cluster started during crepuscular periods. All models predicted ungulate consumption clusters to occur less when clusters were initiated during crepuscular and nocturnal periods compared to daytime. Land designation also influenced behavioural state predictions. According to the habitat, and behaviour and habitat models, vegetation feeding clusters were more likely in the mountains, likely reflecting availability of bear foods (vegetative foods more available than animal foods in the mountains). Lastly, the behaviour model predicted that vegetation feeding with bedding clusters were less likely in the foothills.

Influence of Fix Rate on Behavioural Inferences

Decreasing fix rate from 1-h to 2-h resulted in a mean drop in detection of at least 30% across vegetation feeding, bedding, and vegetation feeding with bedding respectively (Figure 3.2). Further dropping the fix rate to 4-h resulted in less than 40% of clusters still detected for these three behaviours. When the fix rate was dropped to 6-h, a maximum of 25% of clusters were still detected. Further dropping to 8-h resulted in up to 15% of cluster detection, with 12-h fix rate only preserving approximately 10% of clusters. Ungulate feeding behaviour was less sensitive to fix rate decrease, with 80% of ungulate consumption clusters still detected at fix rates of 2-h and 4-h. Further decreases in fix rate resulted in detection below 70%, but even a 12-h fix rate still resulted in detection of almost 50% of ungulate feeding clusters. These relatively high mean retention rates for carcass clusters are even more substantial if only the top ungulate consumption predictive model (behaviour at cluster) is considered.

Influence of Behaviour on Fix Success

Cluster fix success was highest at vegetation feeding sites, averaging 98.1 ± 5.2%. In comparison, fix success at bedding sites was 93.2 ± 10.8%, 92.6 ± 11.3% at vegetation feeding with bedding sites, and 92.3 ± 10.7% at ungulate consumption sites. When I controlled for habitat type, closed habitats (shrub, conifer, and mixed forest) had lower fix success when bears bedded or when they fed on vegetation and bedded, compared to when they fed on vegetation only (Table 3.6). I did not have carcass consumption samples for shrub and mixed forest, but for conifer forest fix success was lower for ungulate consumption behaviour compared to vegetation feeding. In open habitats (barren land, and grassland), fix success was similar across behaviours, except being lower for vegetation feeding and bedding behaviour when compared to vegetation feeding alone. However, the latter pattern should be interpreted with caution as it resulted from a small sample size.

Grizzly Bear Behaviour in a Multiple-use Landscape

Although the four behavioural states considered occurred on all land designations (foothills, mountains, reclaimed mines), frequency of occurrence of these behaviours differed between land designations (Figure 3.3). Only data from the best predictive model for a specific behaviour are reported, but the observed patterns of frequency differences maintained for the other two top models. Based on behavioural state predictions, vegetation feeding differed between land designations (χ^2 = 156.9, df = 2, P < 0.0001), occurring more in the mountains than in the foothills or reclaimed mines, although these results need to be interpreted with caution because of the low accuracy of prediction for vegetation feeding. Frequency of bedding differed between land designations (χ^2 = 474.9, *df* = 2, $P < 0.0001$), with most bedding alone predicted for the foothills. Occurrence of vegetation feeding with bedding also differed between land designations (χ^2 = 245.6, *df* = 2, $P < 0.0001$), being more frequent in the mountains and on reclaimed mines compared to foothills. Finally, ungulate consumption differed by land designation (χ^2 = 79.0, *df* = 2, $P < 0.0001$), with most frequent consumption occurring in the foothills.

DISCUSSION

Identifying behaviour of species that are of conservation concern is an ongoing challenge for researchers working in uncontrolled environmental settings where direct observations are hindered by species rarity, wide ranging patterns and/or habitat characteristics. New GPS technologies allow unforeseen resolution in monitoring animal use of the landscape, but understanding the link between GPS locations and animal behaviour requires a concerted effort of researchers interested in extracting biological information from technological tools. Many advances in the interpretation of behaviour from GPS radiocollar data have come from studies on carnivores, but these have typically focused on distinguishing carnivore predatory events from no kill locations. However, because human activity and associated mortality risk are substantial limiting factors for carnivore populations (Creel and Creel 1998, Andren et al. 2006, Goodrich et al. 2008), behavioural studies and conservation decisions would benefit from obtaining additional information from GPS radiocollar data, such as understanding carnivore behaviour in relation to human land use. This information could for example assist in minimizing human-carnivore encounters, or help mitigate the effects of land use change on carnivore populations.

Following the behaviour-conservation unified framework called for in the recent literature (Blumstein and Fernandez-Juricic 2004, Caro 2007), I applied multinomial logistic regression modelling to a large GPS radiocollar dataset for Alberta grizzly bears in a varied landscape including foothills with high human use, mountains with low human use, and reclaimed mines with low human use but human altered habitat. Habitat variables were not important at predicting ungulate consumption, with cluster characteristics alone providing good carcass site prediction. Once a kill had been made or a carcass located that had been killed by another predator, bears spent more time at the carcass compared to sites with other behaviours.

From a predictive standpoint, because ungulate consumption can be readily identified from cluster patterns without the need for habitat information, model parameters estimated from the top behaviour at cluster model can be used to direct field visitation for studies of grizzly bear ungulate prey composition. Based on the low variability in predictive accuracy (SD 1%), the 48% accuracy of my ungulate consumption predictions also can be used to correct kill rate estimates (by simple multiplication of predicted kills by 2). The resulting estimate will have lowest error for times of the year when bears are predominantly predatory, such as ungulate calving season. The higher incidence of kill clusters in the foothills compared to mountainous areas or reclaimed mines is corroborated by dietary analysis which identified higher ungulate consumption by bears in the foothills (Chapter 4, Munro et al. 2006), as well as supported by the lower ungulate predation risk on grasslands (Hebblewhite et al. 2005) such as reclaimed mines.

Predicting bear bedding alone was best achieved by incorporating habitat variables only, which strengthens previous findings that microsite level habitat variables influence resting-site selection in brown bears (Ordiz et al. 2011). Ability to identify bedding sites is particularly important for carnivores inhabiting areas with extensive human activity, where preservation of fine scale habitat features that favour bedding is required for target species conservation (Te Wong et al. 2004, Purcell et al. 2009). Identifying bedding events in a GPS radiocollar location dataset is a useful endeavour even for studies in which identifying bedding habitats is not prioritized. GPS locations associated with bedding as predicted from the multinomial behavioural state model could be extracted from the dataset, facilitating analyses exclusively for foraging habitat selection. Such an approach should be treated with caution because of the likely connection between foraging and bedding behaviours.

Predicting vegetation feeding with bedding required a complex combination of variables that included behaviour and habitat characteristics and being able to predict where such complex sites occur is important because their conservation can have the double benefit of protecting bedding and foraging habitat. Interestingly, bears foraged and bedded at the same site less in the foothills than in the mountains or on reclaimed mines, possibly reflecting differences in food habits between land designations. Because bears in the foothills have more meat in their diet, plant foods may not influence their activity patterns as much as ungulate distribution. Alternatively, in the foothills bears may be displaced by greater human activity, therefore not spending much time at a site unless they obtain a substantial energetic benefit, such as by consuming an ungulate carcass.

I was unable to predict vegetation feeding when it did not occur in conjunction with bedding. My definition of location clusters required bears to spend ≥3 hours in an area with a radius of up to 50-m for the seed cluster (*sensu* Knopff et al. [2009]). Based on opportunistic direct observations of bears digging for roots and grazing on herbaceous plants (*n* = 10), vegetation feeding does not occur within the above spatial and temporal cluster constraints. The GPS radiocollar fix rate would need to be set at lower intervals than hourly as defined in this study, but one caveat of a more frequent fix rate is that animal movements occurring at such fine temporal scales could be confounded by GPS error, resulting in inference problems at least for elk (Jerde and Visscher 2005). Rapid movement rates of some cursorial carnivores are better suited for more frequent fix rate schedules (McKenzie et al. 2012), and such schedules should be tailored to the research organism under study, preferably after a pilot study with radiocollars set at high fix rate. My simulations involving varying fix rates showed that rates of ≥4 h result in <50% of clusters being detected for all behavioural states, with the exception of kill clusters which are more robust to fix rate decrease (Figure 3.2). Even at a fix rate of 2-h only up to 75% of clusters were detected, with vegetation feeding and bedding clusters being most affected by fix rate decrease. Based on these findings, I recommend a fix rate of 1-h or more frequent for inferring behavioural states of grizzly bears. I recommend study designs that have fix rate schedules which allow behavioural inferences but also minimize the need for animal recapture to replace collars on low battery. If the focus of a study is researching grizzly bear predation on large ungulates, then a 4-h fix rate appears sufficient to preserve a substantial portion of the clusters (80%). Researchers should acknowledge that using such an infrequent fix rate may underrepresent the importance of young and/or small ungulates/other mammals, as well as scavenging by grizzly bears.

Animal behaviour predictions based on GPS radiocollar data can be affected if behaviour influences fix success (Frair et al. 2010). The finding that fix success was highest for vegetation feeding across most habitat categories suggests that behaviourally-induced bias in fix success could affect predictions of animal behaviour. Because I assigned behavioural states and performed habitat categorization based on field visitation, my inferences eliminate spurious effects present in previous studies that attempt to disentangle effects of animal behaviour and land cover on fix success based on behavioural assumptions, and low accuracy GIS habitat data (e.g., 60-90% accuracy for Landsat land cover data [Wickham et al. 2004, Mayaux et al. 2006]).

Despite their ability to incorporate a dependent variable with >2 categories, multinomial models have rarely been applied to data collected during direct field observations of behaviour (Borkowski et al. 2006, Witter et al. 2012), and never to infer behaviour from animal sign data, or for terrestrial carnivores. I demonstrated that such models can be useful to infer behavioural states based on GPS radiocollar technology and behavioural sign, for example prey carcasses, hair, bones, dug up ground, bitten plant stems, or bedding depressions. This approach enables predictions of behavioural states for the entire duration of animal GPS radiocollar monitoring, provided that fix rate, fix success and field protocols for sampling behaviour are adequate. In my field cluster sampling program I was highly successful in attributing behavioural information to location clusters (98.4%), but in framing behavioural states for data analyses I adopted a conservative approach to minimize inaccuracies in prediction. Three types of vegetation feeding data were pooled because of small sample sizes, and carcass sites with or without bedding were combined because bedding events are not reliably identifiable at kill sites, for example if the predator rests directly on the carcass to defend it. Field protocols for cluster visitation should strive to reach a balance between visiting clusters soon after the animal was there, thereby minimizing site disturbance by non-monitored animals, and care not to interfere with animal behaviour. In addition, if the study species is potentially dangerous, visiting the site too early can put field personnel at risk, such as surprising large carnivores feeding or resting at ungulate carcasses.

In my study I was unable to radiocollar all grizzly bears and other large carnivores present in the area including black bears (*Ursus americanus*), wolves (*Canis lupus*) and cougars (*Puma concolor*). Some ungulate consumption events might have been missed if a non-radiocollared carnivore moved the carcass before field crews visited the cluster site. I minimized this problem by performing thorough site investigations looking for evidence of hair, drag marks, carnivore scat and its freshness. An additional potentially confounding issue was the fact that larger bodied grizzly bears have higher per minute meat intakes than smaller bears (Wilmers and Stahler 2002), and I expected that characteristics of individual bears may influence behavioural inferences based on GPS cluster duration. However, models using a random intercept for unique bear identity did not outperform multinomial models, suggesting that my modelling approach was adequate.

Whether facultative or obligate, carnivores display complex behavioural states, and their structural role in ecosystems (Sergio et al. 2008) warrants conservation relevance to behavioural understanding of carnivore ecology. Knowledge of where carnivores perform certain behaviours can be used to identify suitable areas that need protection, at a level of detail beyond the traditional approach of understanding habitat selection based on GPS locations with unknown behaviour. For example, areas where facultative carnivores such as bears consume ungulates are important because they facilitate body mass gain and associated increase in reproductive success (Hilderbrand et al. 1999). In the case of grizzly bears on mined landscapes, which change habitats from forested to artificial open areas, ungulates are consumed in tree patches left undisturbed during mining (Chapter 5). By discriminating multiple behavioural states from telemetry data, my modeling framework enables identification of such areas in need of protection, and is transferable to other species and populations which may experience loss of behaviours (*sensu* Caro and Sherman 2012) as a result of human-caused environmental change.

LITERATURE CITED

Andren, H., J. D. C. Linnell, O. Liberg, R. Andersen, A. Danell, J. Karlsson, J. Odden, P. F. Moa, P. Ahlqvist, T. Kvam, R. Franzen, and P. Segerstrom. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation **131**:23-32.

Barraquand, F., and S. Benhamou. 2008. Animal movements in heterogeneous landscapes: Identifying profitable places and homogeneous movement bouts. Ecology **89**:3336-3348.

Bates, L. A., and R. W. Byrne. 2009. Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*): foraging and border checking. Behavioral Ecology and Sociobiology **64**:247-255.

Blumstein, D. T., and E. Fernandez-Juricic. 2004. The emergence of conservation behavior. Conservation Biology **18**:1175-1177.

Borkowski, J. J., P. J. White, R. A. Garrott, T. Davis, A. R. Hardy, and D. J. Reinhart. 2006. Behavioral responses of bison and elk in Yellowstone to snowmobiles and snow coaches. Ecological Applications **16**:1911-1925.

Boulanger, J., G. B. Stenhouse, M. Proctor, S. Himmer, D. Paetkau, and J. Cranston. 2005. 2004 Population inventory and density estimates for the Alberta 3B and 4B Grizzly bear management area. Report prepared for Alberta Sustainable Resource Development, Fish and Wildlife Division. Integrated Ecological Research, Nelson, BC, Canada.

Boyce, M. S., J. Pitt, J. M. Northrup, A. T. Morehouse, K. H. Knopff, B. Cristescu, and G. B. Stenhouse. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2213-2219.

Byrne, M. E., and M. J. Chamberlain. 2012. Using first-passage time to link behaviour and habitat in foraging paths of a terrestrial predator, the racoon. Animal Behaviour **84**:593-601.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2157-2162.

Caro, T. 2007. Behavior and conservation: a bridge too far? Trends in Ecology and Evolution **22**:394-400.

Caro, T., and P. W. Sherman. 2011. Endangered species and a threatened discipline: behavioural ecology. Trends in Ecology and Evolution **26**:111-118.

Caro, T., and P. W. Sherman. 2012. Vanishing behaviors. Conservation Letters **5**:159-166.

Cattet, M., J. Boulanger, G. Stenhouse, R. A. Powell, and M. L. Reynolds-Hogland. 2008. An evaluation of long-term capture effects in ursids: Implications for wildlife welfare and research. Journal of Mammalogy **89**:973-990.

Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce. 2012. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society B: Biological Sciences **279**:4407-4416.

Creel, S., and N. M. Creel. 1998. Six ecological factors that may limit African wild dogs, *Lycaon pictus*. Animal Conservation **1**:1-9.

Dickson, B. G., J. S. Jenness, and P. Beier. 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. Journal of Wildlife Management **69**:264-276.

Forester, J. D., A. R. Ives, M. G. Turner, D. P. Anderson, D. Fortin, H. L. Beyer, D. W. Smith, and M. S. Boyce. 2007. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs **77**:285-299.

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., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology **20**:273-287.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2187-2200.

Fryxell, J. M., M. Hazell, L. Borger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proceedings of the National Academy of Sciences, USA **105**:19114-19119.

Gillingham, M. P., and D. R. Klein. 1992. Late-winter activity patterns of moose (*Alces alces gigas*) in Western Alaska. Canadian Journal of Zoology **70**:293-299.

Goodrich, J. M., L. L. Kerley, E. N. Smirnov, D. G. Miquelle, L. McDonald, H. B. Quigley, M. G. Hornocker, and T. McDonald. 2008. Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. Journal of Zoology **276**:323-329.

Graves, T. A., and J. S. Waller. 2006. Understanding the causes of missed Global Positioning System telemetry fixes. Journal of Wildlife Management **70**:844-851.

Hayward, M., G. Hayward, D. Druce, and G. Kerley. 2009. Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. Biodiversity and Conservation **18**:887-904.

Heard, D. C., L. M. Ciarniello, and D. R. Seip. 2008. Grizzly bear behavior and Global Positioning System collar fix rates. Journal of Wildlife Management **72**:596-602.

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

Hebblewhite, M., and D. T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2303-2312.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology **77**:132-138.

Huberty, C. J. 1994. Applied discriminant analysis. Wiley and sons, New York.

Jerde, C. L., and D. R. Visscher. 2005. GPS measurement error influences on movement model parametrization. Ecological Applications **15**:806-810.

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

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.

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

Loettker, P., A. Rummel, M. Traube, A. Stache, P. Sustr, J. Mueller, and M. Heurich. 2009. New possibilities of observing animal behaviour from a distance using activity sensors in GPS-collars: an attempt to calibrate remotely collected activity data with direct behavioural observations in red deer *Cervus elaphus*. Wildlife Biology **15**:425-434.

Martin, P., and P. Bateson. 2007. Measuring behaviour: an introductory guide. Cambridge University Press, Cambridge, UK.

Mattisson, J., H. Andren, J. Persson, and P. Segerstrom. 2010. Effects of species behavior on Global Positioning System collar fix rates. Journal of Wildlife Management **74**:557-563.

Mayaux, P., H. Eva, J. Gallego, A. H. Strahler, M. Herold, S. Agrawal, S. Naumov, E. E. De Miranda, C. M. Di Bella, C. Ordoyne, Y. Kopin, and P. S. Roy. 2006. Validation of the global land cover 2000 map. Ieee Transactions on Geoscience and Remote Sensing **44**:1728-1739.

McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter predator movement and the functional response. Interface Focus **2**:205-216.

Merrill, E., H. k. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair. 2010. Building a mechanistic understanding of predation with GPS-based movement data. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2279-2288.

Mueller, T., and W. F. Fagan. 2008. Search and navigation in dynamic environments - from individual behaviors to population distributions. Oikos **117**:654-664.

Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy **87**:1112-1121.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences, USA **105**:19052-19059.

Nielsen, S. E., and A. Haney. 1998. Gradient responses for understory species in a bracken grassland and northern dry forest ecosystem of Northeast Wisconsin. Transactions of the Wisconsin Academy of Sciences Arts and Letters **86**:149-166.

Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004. Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management **199**:51-65.

Ordiz, A., O.-G. Stoen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia **166**:59-67.

Pitman, R. T., L. H. Swanepoel, and P. M. Ramsay. 2012. Predictive modelling of leopard predation using contextual Global Positioning System cluster analysis. Journal of Zoology **288**:222-230.

Purcell, K. L., A. K. Mazzoni, S. R. Mori, and B. B. Boroski. 2009. Resting structures and resting habitat of fishers in the southern Sierra Nevada, California. Forest Ecology and Management **258**:2696-2706.

Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step selection functions. Ecography **33**:1113-1122.

Sand, H., B. Zimmermann, 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.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters **11**:1338-1350.

Sergio, F., T. Caro, D. Brown, B. Clucas, J. Hunter, J. Ketchum, K. McHugh, and F. Hiraldo. 2008. Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. Annual Review of Ecology Evolution and Systematics **39**:1-19.

Shamoun-Baranes, J., R. Bom, E. E. van Loon, B. J. Ens, K. Oosterbeek, and W. Bouten. 2012. From sensor data to animal behaviour: An oystercatcher example. PLoS ONE **7**:e37997.

Tambling, C. J., E. Z. Cameron, J. T. Du Toit, and W. M. Getz. 2010. Methods for locating African lion kills using Global Positioning System movement data. Journal of Wildlife Management **74**:549-556.

Tambling, C. J., S. D. Laurence, S. E. Bellan, E. Z. Cameron, J. T. du Toit, and W. M. Getz. 2012. Estimating carnivoran diets using a combination of carcass observations and scats from GPS clusters. Journal of Zoology **286**:102-109.

Te Wong, S., C. W. Servheen, and L. Ambu. 2004. Home range, movement and activity patterns, and bedding sites of Malayan sun bears *Helarctos malayanus* in the Rainforest of Borneo. Biological Conservation **119**:169-181.

Turchin, P. 1998. Quantitative analysis of movement: Measuring and modeling population redistribution in animals and plants. Sinaeuer Associates, Sunderland, MA, USA.

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.

Wickham, J. D., S. V. Stehman, J. H. Smith, and L. Yang. 2004. Thematic accuracy of the 1992 National Land-Cover Data for the western United States. Remote Sensing of Environment **91**:452-468.

Wilmers, C. C., and D. R. Stahler. 2002. Constraints on active-consumption rates in gray wolves, coyotes, and grizzly bears. Canadian Journal of Zoology **80**:1256.

Wittemyer, G., L. Polansky, I. Douglas-Hamilton, and W. M. Getz. 2008. Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. Proceedings of the National Academy of Sciences, USA **105**:19108-19113.

Witter, L. A., C. J. Johnson, B. Croft, A. Gunn, and M. P. Gillingham. 2012. Behavioural trade-offs in response to external stimuli: time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. Journal of Animal Ecology **81**:284-295.

Zheng, B. Y., and A. Agresti. 2000. Summarizing the predictive power of a generalized linear model. Statistics in Medicine **19**:1771-1781.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, USA.

Table 3.1: Model structure and deviance for multinomial models predicting grizzly bear behaviour at GPS radiocollar location clusters in west-central Alberta, Canada (2008-2010). Top models for each candidate set are reported, as these were the only models that received support (w_i = 1.00 and $\Delta\text{AIC}_c < 10$). The null model also is reported for comparison. Model complexity (number of parameters) is given by K_i, and deviance is given by -2LL. Model sets included *a priori* variable combinations with/without season, time of day and land class.

Model set		**Variables**	K_i	**-2LL**	AIC_c	Δ_i	w_i	**% Dev. explained**
Behaviour	Top	Points_{cl} + 24h_{cl} + Fidelity_{cl} + Avg_dist_{cl} + Season + Time_day + Land_class	8	899.7	916.0	0.0	1.00	27.8
	Null		1	1246.5	1248.5	332.5	0.00	0.0
Habitat	Top	Habitat_class + Slope + Slope^2 + SSI + Season + Time_day + Land_class	8	1029.5	1045.8	0.0	1.00	17.4
	Null		1	1246.5	1248.5	202.8	0.00	0.0
Behaviour + Habitat	Top	Points_{cl} + 24h_{cl} + Fidelity_{cl} + Avg_dist_{cl} + Habitat_class + Slope + Slope^2 + SSI + Season + Time_day + Land_class	12	801.5	826.1	0.00	1.00	35.7
	Null		1	1246.5	1248.5	422.4	0.00	0.0

% Dev. explained - percentage deviance explained

Table 3.2: Proportion of the true composition of grizzly bear behavioural states predicted by top multinomial models for behaviour at cluster, habitat at cluster, and behaviour and habitat at cluster. Data were acquired in 2008-2010 in west-central Alberta, and randomly partitioned (*n* = 4) without replacement. A value of 1.00 represents correct prediction.

Model	**Behavioural state**	**Partition 1**	**Partition 2**	**Partition 3**	**Partition 4**	**Mean**	**SD**
Behaviour at cluster	Veg w/o Bed	0.00	0.00	0.05	0.00	0.01	0.03
	Bed	0.39	0.00	0.75	0.48	0.40	0.31
	Veg w Bed	0.61	0.90	0.50	0.50	0.63	0.19
	Carcass w or w/o Bed	0.48	0.48	0.48	0.47	0.48	0.01
Habitat at cluster	Veg w/o Bed	0.38	0.00	0.32	0.00	0.18	0.20
	Bed	0.97	0.56	0.92	0.54	0.75	0.23
	Veg w Bed	0.00	0.70	0.23	0.61	0.38	0.33
	Carcass w or w/o Bed	0.04	0.00	0.00	0.00	0.01	0.02
Behaviour & Habitat at cluster	Veg w/o Bed	0.08	0.00	0.26	0.00	0.09	0.12
	Bed	0.37	0.00	0.53	0.37	0.32	0.22
	Veg w Bed	0.65	0.95	0.82	0.78	0.80	0.12
	Carcass w or w/o Bed	0.37	0.31	0.32	0.22	0.31	0.06

Veg - vegetation feeding site (root digging, grazing, berry foraging)

Bed - bedding/resting site

Carcass - mammal carcass

w - with

w/o – without

Table 3.3: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for the top multinomial model based on behaviour at cluster, as assessed by Δ_i and w_i. Estimates for which the [CI] did not overlap zero are given in bold. Bedding behaviour was withheld as a reference category in the dependent variable. For the independent variables, barren/herbaceous class (Habitat), spring (Season), diurnal (Time_day) and reclaimed mine (Land_class) were withheld as reference categories.

Variable		**Vegetation feeding**				**Vegetation feeding with Bedding**				**Ungulate carcass w/without Bedding**			
		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
				Lower	Upper			Lower	Upper			Lower	Upper
Cluster													
	Points_{cl}	**−0.543**	**0.105**	**−0.750**	**−0.337**	**0.092**	**0.045**	**0.003**	**0.181**	**0.157**	**0.049**	**0.061**	**0.254**
	24h_{cl}	−1.185	0.639	−2.437	0.067	0.320	0.522	−0.703	1.343	−0.594	0.483	−1.541	0.353
	Fidelity_{cl}	0.003	0.008	−0.013	0.020	−0.002	0.003	−0.008	0.004	**−0.007**	**0.003**	**−0.013**	**−0.000**
	Avg_dist_{cl}	**0.123**	**0.033**	**0.058**	**0.188**	−0.031	0.026	−0.082	0.020	**−0.073**	**0.027**	**−0.127**	**−0.020**
Season													
	Summer	**−0.939**	**0.443**	**−1.807**	**−0.071**	0.142	0.374	−0.590	0.874	−0.494	0.360	−1.200	0.212
	Fall	**−1.708**	**0.552**	**−2.790**	**−0.626**	0.091	0.368	−0.631	0.813	**−1.042**	**0.380**	**−1.787**	**−0.297**
Time_day													
	Crepuscular	0.194	0.528	−0.840	1.228	**0.824**	**0.368**	**0.103**	**1.545**	**−1.266**	**0.495**	**−2.236**	**−0.296**
	Nocturnal	−0.805	0.463	−1.712	0.101	0.176	0.322	−0.456	0.807	**−1.014**	**0.382**	**−1.763**	**−0.265**
Land_class													
	Foothills	−0.661	0.548	−1.736	0.414	**−1.072**	**0.389**	**−1.834**	**−0.310**	−0.157	0.447	−1.032	0.719
	Mountains	0.480	0.490	−0.480	1.439	−0.120	0.370	−0.845	0.605	−0.759	0.522	−1.782	0.264

Table 3.4: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for the top multinomial model based on habitat at cluster, as assessed by Δ_i and w_i. Estimates for which the [CI] did not overlap zero are given in bold. Bedding behaviour was withheld as a reference category in the dependent variable. For the independent variables, barren/herbaceous class (Habitat), spring (Season), diurnal (Time_day) and reclaimed mine (Land_class) were withheld as reference categories.

Variable		**Vegetation feeding**				**Vegetation feeding with Bedding**				**Ungulate carcass w/without Bedding**			
		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
				Lower	Upper			Lower	Upper			Lower	Upper
Habitat													
	Shrub	0.711	0.781	−0.819	2.241	−0.451	0.579	−1.585	0.684	0.121	0.768	−1.384	1.627
	Conifer forest	**−2.295**	**0.649**	**−3.567**	**−1.023**	**−1.706**	**0.453**	**−2.593**	**−0.818**	−0.260	0.587	−1.411	0.890
	Mixed forest	−0.909	0.885	−2.643	0.825	−0.259	0.628	−1.491	0.973	0.080	0.699	−1.290	1.449
	Slope	−0.021	0.031	−0.081	0.040	0.024	0.020	−0.015	0.062	**−0.040**	**0.018**	**−0.076**	**−0.004**
	Slope^2	0.000	0.000	−0.001	0.001	−0.000	0.000	−0.001	0.000	0.000	0.000	−0.001	0.001
	SSI	−0.387	0.263	−0.903	0.128	0.079	0.225	−0.362	0.521	0.113	0.304	−0.483	0.709
Season													
	Summer	0.095	0.417	−0.723	0.913	0.149	0.375	−0.586	0.884	**−0.664**	**0.315**	**−1.282**	**−0.047**
	Fall	**−1.508**	**0.562**	**−2.610**	**−0.406**	0.205	0.383	−0.547	0.956	**−0.958**	**0.348**	**−1.640**	**−0.277**
Time_day													
	Crepuscular	−0.080	0.559	−1.175	1.015	0.662	0.375	−0.074	1.397	**−1.269**	**0.447**	**−2.145**	**−0.392**
	Nocturnal	−0.846	0.443	−1.716	0.023	−0.042	0.318	−0.665	0.581	**−1.192**	**0.294**	**−1.769**	**−0.615**
Land_class													
	Foothills	−0.192	0.712	−1.587	1.204	−0.141	0.462	−1.046	0.763	0.208	0.486	−0.745	1.161
	Mountains	**1.419**	**0.647**	**0.150**	**2.687**	0.630	0.439	−0.230	1.490	−0.338	0.503	−1.323	0.648

Table 3.5: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for the top multinomial model based on behaviour and habitat at cluster, as assessed by Δ_i and w_i. Estimates for which the [CI] did not overlap zero are given in bold. Bedding behaviour was withheld as a reference category in the dependent variable. For the independent variables, barren/herbaceous class (Habitat), spring (Season), diurnal (Time_day) and reclaimed mine (Land_class) were withheld as reference categories.

Variable		**Vegetation feeding**				**Vegetation feeding with Bedding**				**Ungulate carcass w/without Bedding**			
		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
				Lower	Upper			Lower	Upper			Lower	Upper
Cluster													
	Points$_{cl}$	**−0.613**	**0.133**	**−0.873**	**−0.353**	**0.103**	**0.046**	**0.012**	**0.194**	**0.153**	**0.049**	**0.057**	**0.250**
	24h$_{cl}$	−0.634	0.776	−2.154	0.887	0.555	0.563	−0.548	1.658	−0.586	0.484	−1.535	0.363
	Fidelity$_{cl}$	0.001	0.009	−0.016	0.019	−0.002	0.003	−0.008	0.004	**−0.006**	**0.003**	**−0.013**	**−0.000**
	Avg_dist$_{cl}$	**0.156**	**0.039**	**0.080**	**0.232**	−0.013	0.027	−0.067	0.040	−0.053	0.028	−0.108	0.003
Habitat													
	Shrub	0.538	1.015	−1.450	2.527	−0.440	0.591	−1.598	0.717	−0.462	1.189	−2.793	1.868
	Conifer forest	**−3.168**	**0.875**	**−4.883**	**−1.452**	**−1.744**	**0.469**	**−2.664**	**−0.824**	−0.458	0.639	−1.710	0.794
	Mixed forest	−1.402	0.960	−3.282	0.479	−0.269	0.653	−1.548	1.011	−0.051	0.846	−1.709	1.607
	Slope	−0.018	0.033	−0.082	0.047	0.023	0.019	−0.016	0.061	−0.029	0.025	−0.078	0.019
	Slope^2	0.000	0.000	−0.001	0.001	−0.000	0.000	−0.001	0.003	−0.000	0.000	−0.001	0.001
	SSI	−0.313	0.319	−0.939	0.312	0.060	0.221	−0.374	0.494	0.281	0.397	−0.497	1.059
Season													
	Summer	**−1.076**	**0.529**	**−2.113**	**−0.038**	0.346	0.384	−0.406	1.098	−0.535	0.365	−1.250	0.181
	Fall	**−2.761**	**0.676**	**−4.086**	**−1.436**	0.256	0.384	−0.497	1.010	**−1.201**	**0.400**	**−1.985**	**−0.416**
Time_day													
	Crepuscular	0.037	0.674	−1.284	1.359	0.715	0.380	−0.029	1.459	**−1.434**	**0.541**	**−2.494**	**−0.375**
	Nocturnal	−0.927	0.483	−1.873	0.019	0.110	0.348	−0.572	0.791	**−1.050**	**0.364**	**−1.762**	**−0.337**
Land_class													
	Foothills	0.721	0.887	−1.017	2.459	−0.309	0.484	−1.257	0.638	−0.295	0.561	−1.395	0.805
	Mountains	**2.170**	**0.845**	**0.513**	**3.827**	0.560	0.434	−0.291	1.410	−0.389	0.587	−1.540	0.762

Table 3.6: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for GLM models illustrating GPS radiocollar fix success as a function of grizzly bear behavioural state. Separate models were run for each of four broad habitat categories, using data collected during field visitation as input. Results of all four models are presented in the same table. Estimates for which the confidence intervals did not overlap zero are given in bold. Vegetation feeding was withheld as a reference category in the dependent variable.

		Bedding				**Vegetation feeding with Bedding**				**Ungulate carcass with/without Bedding**			
Variable		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
				Lower	Upper			Lower	Upper			Lower	Upper
Habitat													
Model 1	Barren/ Herbaceous	−1.940^	0.815	−1.597	1.597	**−17.043^**	**0.966**	**−18.937**	**−15.149**	−1.940^	1.262	−2.474	2.474
Model 2	Shrub	**−17.752**	**0.642**	**−19.010**	**−16.494**	**−16.483**	**0.896**	**−18.239**	**−14.727**				
Model 3	Conifer forest	**−14.699**	**0.648**	**−15.969**	**−13.430**	**−15.511**	**0.736**	**−16.954**	**−14.068**	**−14.225**	**1.064**	**−16.311**	**−12.140**
Model 4	Mixed forest	**−16.883**	**1.198**	**−19.231**	**−14.536**	**−16.296**	**1.140**	**−18.530**	**−14.061**				

^ Coefficient reported at 10^9 times its original value

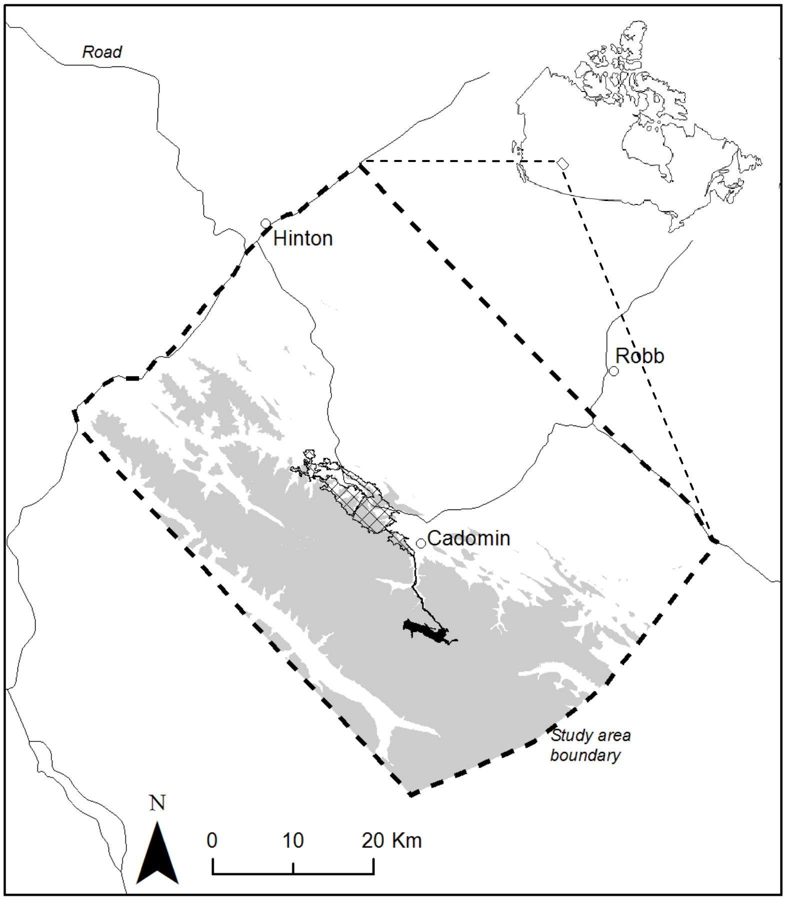

Figure 3.1: Study area for grizzly bear behaviour in west-central Alberta, Canada, including major roads, towns (empty dots) and colour coded mine disturbance areas: reclaimed mines (crosshatch), active mine (black). Shading within study area boundary (dashed line) represents Mountains (≥1,700 m; gray) with the rest being foothills (<1,700 m; white).

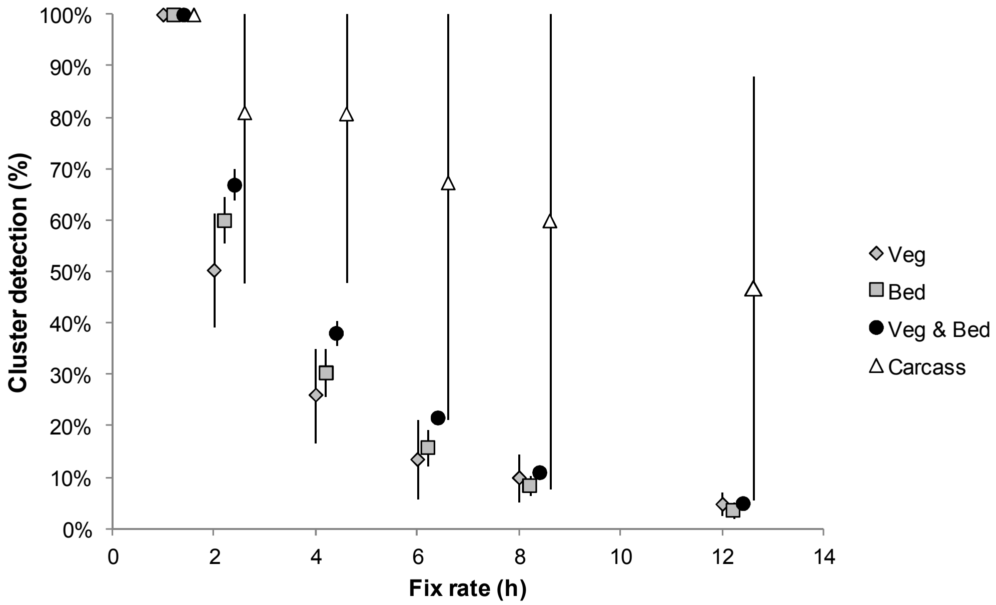

Figure 3.2: Detectability of grizzly bear behavioural states from location clusters in west-central Alberta, based on manipulating GPS radiocollar fix rates. Error bars are standard deviations calculated based on top models for each set of candidate models (behavioural, habitat, behaviour and habitat). Veg – vegetation feeding, Bed – bedding, Carcass – ungulate carcass consumption.

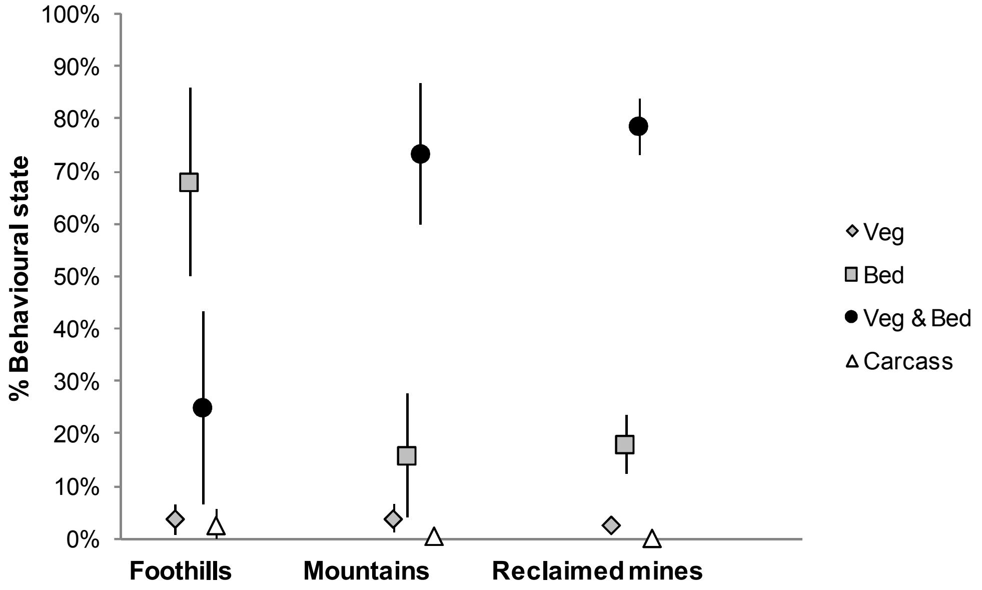

Figure 3.3: Proportion of grizzly bear behaviours by land designation, based on predictions from multinomial logit models with behavioural state as categorical dependent variable. Error bars are standard deviations calculated based on top models for each set of candidate models (behavioural, habitat, behaviour and habitat). Veg – vegetation feeding, Bed – bedding, Carcass – ungulate carcass consumption.

SUPPLEMENTARY MATERIAL

Table S.1: Model structure and deviance for candidate multinomial models (behaviour at cluster set) predicting bear behaviour at GPS radiocollar location clusters in west-central Alberta, Canada. Model complexity (number of parameters) is given by K_i, and deviance is given by -2LL. Model sets included *a priori* variable combinations with/without season, time of day and land class.

Model	**Variables**	K_i	**-2LL**	**AIC$_c$**	Δ_i	w_i	**% Dev. explained**
Top	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Season + Time_day + Land_class	8	899.7	916.0	0.0	1.00	27.8
	Points$_{cl}$ + Season + Time_day + Land_class	5	942.9	953.1	37.0	0.00	24.4
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Time_day	6	942.9	955.0	39.0	0.00	24.4
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Season	6	955.0	967.2	51.2	0.00	23.4
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Land_class	6	956.8	969.0	53.0	0.00	23.2
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$	5	984.8	994.9	78.9	0.00	21.0
	Points$_{cl}$	1	1030.8	1032.9	116.9	0.00	17.3
	24h$_{cl}$ + Season + Time_day + Land_class	5	1051.7	1061.9	145.8	0.00	15.6
	Avg_dist$_{cl}$ + Season + Time_day + Land_class	5	1127.6	1137.8	221.7	0.00	9.5
	Fidelity$_{cl}$ + Season + Time_day + Land_class	5	1128.8	1138.9	222.9	0.00	9.4
	24h$_{cl}$	1	1149.4	1151.5	235.4	0.00	7.8
	Avg_dist$_{cl}$	1	1238.4	1240.4	324.4	0.00	0.7
	Fidelity$_{cl}$	1	1241.3	1243.4	327.4	0.00	0.4
Null		1	1246.5	1248.5	332.5	0.00	0.0

% Dev. explained - percentage deviance explained

Table S.2: Model structure and deviance for candidate multinomial models (habitat at cluster set) predicting bear behaviour at GPS radiocollar location clusters in west-central Alberta. Model complexity (number of parameters) is given by K_i, and deviance is given by -2LL. Model sets included *a priori* variable combinations with/without season, time of day and land class.

Model	**Variables**	K_i	**-2LL**	**AIC$_c$**	Δ_i	w_i	**% Dev. explained**
Top	Habitat_class + Slope + Slope^2 + SSI + Season + Time_day + Land_class	8	1029.5	1045.8	0.0	1.00	17.4
	Habitat_class + Season + Time_day + Land_class	5	1069.3	1079.4	33.6	0.00	14.2
	Habitat_class + Slope + Slope^2 + SSI + Time_day	6	1075.6	1087.7	41.9	0.00	13.7
	Habitat_class + Slope + Slope^2 + SSI + Season	6	1092.3	1104.5	58.7	0.00	12.4
	Slope + Slope^2 + Season + Time_day + Land_class	6	1093.9	1106.1	60.3	0.00	12.3
	Habitat_class + Slope + Slope^2 + SSI + Land_class	6	1099.9	1112.0	66.2	0.00	11.8
	Habitat_class + Slope + Slope^2 + SSI	5	1127.0	1137.1	91.3	0.00	9.6
	SSI + Season + Time_day + Land_class	5	1132.0	1142.1	96.3	0.00	9.2
	Habitat_class	2	1178.9	1182.9	137.1	0.00	5.4
	Slope + Slope^2	3	1194.7	1200.8	155.0	0.00	4.2
Null		1	1246.5	1248.5	202.8	0.00	0.0
	SSI	2	1244.6	1248.7	202.9	0.00	0.2

% Dev. explained - percentage deviance explained

Table S.3: Model structure and deviance for candidate multinomial models (behaviour and habitat at cluster set) predicting bear behaviour at GPS radiocollar location clusters in west-central Alberta. Model complexity (number of parameters) is given by K_i, and deviance is given by -2LL. Model sets included *a priori* variable combinations with/without season, time of day and land class.

Model	**Variables**	K_i	**-2LL**	**AIC$_c$**	Δ_i	w_i	**% Dev. explained**
Top	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI + Season + Time_day + Land_class	12	801.5	826.1	0.00	1.00	35.7
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Habitat_class + Season + Time_day + Land_class	9	835.3	853.6	27.5	0.00	33.0
	Points$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI + Season + Time_day + Land_class	9	853.6	871.9	45.8	0.00	31.5
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI + Season	10	854.6	875.0	48.9	0.00	31.5
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI + Time_day	10	854.8	875.2	49.1	0.00	31.4
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Slope + Slope^2 + Season + Time_day + Land_class	10	874.4	894.8	68.7	0.00	29.9
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI + Land_class	10	879.3	899.7	73.6	0.00	29.5
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI	9	894.3	912.7	86.6	0.00	28.3
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + SSI+ Season + Time_day + Land_class	9	898.3	916.7	90.6	0.00	27.9
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Habitat_class	6	923.7	935.9	109.8	0.00	25.9
	Points$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI	6	941.9	954.1	128.0	0.00	24.4
	24h$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI + Season + Time_day + Land_class	9	948.0	966.4	140.3	0.00	24.0
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + Slope + Slope^2	7	955.1	969.4	143.3	0.00	23.4
	Points$_{cl}$ + 24h$_{cl}$ + Fidelity$_{cl}$ + Avg_dist$_{cl}$ + SSI	6	983.1	995.3	169.2	0.00	21.1
	Avg_dist$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI + Season + Time_day + Land_class	9	1020.4	1038.8	212.7	0.00	18.1
	Fidelity$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI + Season + Time_day + Land_class	9	1025.1	1043.5	217.3	0.00	17.8
	24h$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI	6	1037.2	1049.3	223.2	0.00	16.8
	Avg_dist$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI	6	1114.6	1126.8	300.7	0.00	10.6
	Fidelity$_{cl}$ + Habitat_class + Slope + Slope^2 + SSI	6	1121.2	1133.3	307.2	0.00	10.1
Null		1	1246.5	1248.5	422.4	0.00	0.0

% Dev. explained - percentage deviance explained

CHAPTER 4

LARGE CARNIVORE ADAPTATION TO INDUSTRIAL LANDSCAPES: GRIZZLY BEAR DIET SWITCHING ON RECLAIMED MINES

ABSTRACT

Industrial developments and reclamation result in habitat change, thereby possibly altering the distribution and availability of food resources for ursids and other large carnivores. Such industrial development is occurring at unprecedented rates in west-central Alberta, Canada, where I monitored the diet of a low-density population of grizzly bears (*Ursus arctos*) occupying a landscape with several large open-pit coal mines. During 2009-2010, 10 adult grizzly bears were instrumented with GPS radiocollars and their diet was compared on reclaimed coal mines, foothills, and Rocky Mountains eastern slopes. In addition, I compared my data with historical bear diet for the same population. Frequency of occurrence and biomass of foods in grizzly bear scats (n = 331) differed substantially between reclaimed mines and areas outside mines. Diet on mines was dominated by non-native forbs and graminoids, while diets in the foothills and mountains consisted primarily of ungulates and *Hedysarum* spp. roots respectively, showing diet switching in accordance with food type availability which differed by land designation. Field visitation of feeding sites identified using GPS relocation clusters (n = 234) also showed that ungulates, primarily moose (*Alces alces*) and elk (*Cervus elaphus*), were the main diet component in the foothills, whereas on reclaimed mines bears were least carnivorous. These dietary differences between land designations illustrate a shift to feeding on non-native forbs while historical diet records reveal emergence of elk as an important bear food in the region. Food resources on reclaimed mines attract bears from nearby wilderness areas and grizzly bears may be more adaptable to landscape change than previously thought. Protection of areas used by bears, whether natural or reclaimed, along with implementation of access management for

recreation vehicles, will facilitate grizzly bear population persistence by decreasing direct human-caused mortality. The grizzly bear's ready use of non-native plant foods on open-pit mines cautions the universal view of this species as a keystone promoter of wilderness.

INTRODUCTION

Knowledge of food webs and habitat use is central to animal ecology (Johnson 1980, Fretwell 1987, Stephens and Krebs 1987), with occurrence and persistence of many animal populations largely determined by the availability and distribution of food and habitat resources (Manly et al. 2002, Stephens et al. 2007). Animals have evolved strategies to exploit certain foods and the decisions on which items to consume and where to search for them are part of foraging theory (Schoener 1971, Pyke et al. 1977). To avoid starvation, animals must be able to track information on food distribution (Dall and Johnstone 2002, Dall et al. 2005). Locating adequate food resources can be challenging when original habitat is changed by human-caused landscape alteration. Loss of habitat has been identified as the major global threat for persistence of animals species and biodiversity conservation (Brooks et al. 2002, Fahrig 2003, Visconti et al. 2011). As human populations increase, so does the consumptive footprint (Houghton 1994) even at lowered population growth rates (Ehrlich et al. 1999), leading to conversion of natural areas to industrially and agriculturally modified landscapes (DeFries et al. 2004, Foley et al. 2005).

Canada is no exception to the global conservation crisis, with habitat loss being the single most important threat to species persistence (Venter et al. 2006). Extractive industries such as open-pit mining are forecasted to expand substantially in response to high demand from rapidly growing world economies (MiHR 2010). Following mine closure, often a principal goal of open-pit mine reclamation is provision of habitat for wildlife (Erickson 1995, Kennedy 2002). In this context, reclaimed mines are accepted as dynamic landscapes (re)colonized by species from nearby undisturbed areas (Hobbs and Harris 2001, Choi et al.

2008). Colonization of mines by focal species is commonly used as a measure of reclamation success (Scott et al. 2001, Cristescu et al. 2012). Terrestrial focal species chosen are typically plants, invertebrates, amphibians, reptiles and birds (McCoy and Mushinsky 2002, Cristescu et al. 2012). Small mammals (Larkin et al. 2008) and ungulates (e.g., Jansen et al. 2009) are less commonly selected, although in natural systems, foraging by ungulates can slow ecological succession (Mysterud 2006) and substantially alter ecological processes (Frank 1998). On reclaimed mines, ungulate foraging also slows or even prevents ecological succession to a more natural vegetation community, especially when combined with harsh abiotic conditions characteristic of mined landscapes (Smyth 1997, Paschke et al. 2003, del Moral et al. 2007) and low dispersal and competitive abilities of native plants compared to non-natives (Holl 2002, Zipper et al. 2011).

If ungulates are killed by carnivores on reclaimed mines, then carnivores could facilitate ecological succession thus helping conversion of mines back to a more natural ecosystem state. However, data on large carnivore diet on reclaimed mines are absent from the peer-reviewed literature. This is not surprising given the difficulty of monitoring such naturally rare species (Colinvaux 1979) with wide-ranging patterns and low probability of detection (McDonald 2004). Nonetheless, their essential role in ecosystem structuring and as potential initiators of trophic cascades makes carnivores a crucial component of the landscape (Soule et al. 2003, Sergio et al. 2008, Estes et al. 2011) and implies their value in gauging reclamation success.

To provide insights into large carnivore adaptation to industrially exploited and subsequently reclaimed areas, I researched grizzly bear feeding ecology on a landscape with open-pit mines in west-central Alberta, Canada. Threats to grizzly bear persistence associated with low population estimates, human-caused mortality and its connection with increased access because of industrial expansion (Nielsen et al. 2004) led to grizzly bear designation as threatened in Alberta in 2010. As the largest terrestrial facultative carnivore in Canada and all of North America, the grizzly bear is arguably the most affected by habitat loss and fragmentation (Weaver et al. 1996), with the species' distribution driven primarily by foods and human persecution (Mattson and Merrill 2002, Laliberte and Ripple 2004, Proctor et al. 2012). The carnivorous digestive system and poor ability to digest plant matter (Schwab et al. 2009, Schwab et al. 2011) suggest that although bears consume vegetation, meat is an important component in their diet. In Yellowstone National Park, grizzly bears have greater consequences on elk (*Cervus elaphus*) calf survival than wolves and other predators (Barber-Meyer et al. 2008), and substantial predatory impact by grizzly bears has been documented in Alaska (Ballard et al. 1990) and Yukon (Larsen et al. 1989). In addition, grizzly bears frequently scavenge on wolf (*Canis lupus*), cougar (*Puma concolor*) and human hunter-killed ungulates (Chapter 5).

My research was conducted on and adjacent to two coal surface mines in west-central Alberta, where Munro et al. (2006) found that grizzly bears consumed a variety of food items. However that study occurred during 2001-2003, when mine reclamation had lower extent. The study did not explicitly address bear diet on reclaimed mines or differences in food consumption on versus outside mines, and did not provide a detailed assessment of food availability on mines, in the mountains and foothills. Nonetheless, Munro et al. (2006) offered an opportunity to investigate changes in diet within the same bear population that I studied during 2009-2010 after the mines had been largely reclaimed.

I summarize frequency of occurrence and biomass of different food items in bear diet using two methods (scat analysis, and GPS location cluster visitation), comparing reclaimed mines to neighbouring foothills and mountains with no mine development. I propose a framework for food intake estimation for complex diets and discuss findings based on availability of foods on versus outside mines, and in relation to past bear diet in the region. Given the threatened status of grizzly bears in Alberta and continuing industrial development, documenting how bears have adapted their diet to modification in the availability of foods associated with mine reclamation is certainly relevant to conservation of this species.

METHODS

Study Area

The 3,200 km^2 study area is located in the province of Alberta (approximate central coordinates 53°05' N 117°25' W), at the eastern edge of the current distributional range of grizzly bears in southern Canada (Proctor et al. 2012) (Figure 4.1). Much of the province is a coal-bearing basin (Cameron and Smith 1991) and Alberta is the largest coal-producing and coal-consuming province in Canada (World Energy Council 2010). Elevation and ruggedness are greater in the western section of the study area which is located on the eastern slopes of the Rocky Mountains, with the eastern section being characterised by a rolling landscape in the foothills. The main natural land cover in the region is coniferous forest dominated by white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*) with deciduous forest composed of balsam polar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*).

Mountainous areas include protected land and generally have less human activity than the foothills. The entire area is sparsely populated and the primary human activity is open-pit coal mining, with other activities including oil and gas development, forest harvesting and recreation. The area encompasses two adjacent reclaimed open pit coal mines (Luscar and Gregg River) located near the coal mining Hamlet of Cadomin (population 60) and an active mine located approximately 20 km south of Cadomin. During the active mining phase, trees and other vegetation are removed, with blasting and excavating occurring to extract coal. Following mine closure, a combination of native non-native forbs and graminoids are sown as part of mine reclamation resulting in a predominantly open landscape with scattered forest fragments left undisturbed during mining. The total combined mine disturbance area for the two mines under study is 3,635 ha (Karmacharya et al. 2011). Human activity is absent from one mine and restricted to <17% of the area of the second mine.

Study Animals

In 2008-2010, I captured and deployed remotely downloadable GPS radiocollars (Telus UHF; Followit, Lindesberg, Sweden) on twelve adult grizzly bears in the study area, with assistance from the Foothills Research Institute Grizzly Bear Program (Hinton, Alberta). An effort was made to sample the bear population randomly on reclaimed mines, foothills (elevation <1,700 m) and mountains (≥1,700 m), using aerial (helicopter darting) and ground capture methods (culvert traps and limited leg-hold snaring) (Cattet et al. 2008). Two large male bears dropped their collars within a month from capture and were excluded from analyses. The remaining ten bears ($n_{males} = 4$; $n_{females} = 5$; $n_{females\ with\ cubs} = 2$) were monitored for a total of 55.6 bear-months (mean ± SD, 5.6 ± 3.3). This sample size (n = 10) represented a considerable proportion of the bear population in the 3,200 km^2 study area, which has 4.79 grizzly bears/1,000 km^2 (Boulanger et al. 2005). One female counted as a female with cubs in 2009 and single female in 2010 for statistical analyses. Radiocollars acquired a GPS location every hour during the active bear season (outside denning). Each month I approached every bear on foot or via fixed-wing aircraft or helicopter and triggered its radiocollar to send GPS data remotely via VHF transmission. During April-October 2009 and 2010, eight of the ten adult grizzly bears tracked used reclaimed mine sites.

Scat Collection and Analysis

Collection of scat occurred at GPS clusters visited in the field, which were identified by running an algorithm designed by Knopff et al. (2009), modified to accommodate a 50-m seed cluster radius. Only clusters with ≥3 telemetry relocations were visited. Due to logistical limitations, for each bear during each month I attempted to visit the largest four GPS relocation clusters as well as randomly picked other clusters from the remaining cluster list as identified by the algorithm. This sampling scheme was designed as a trade-off between enhancing the probability of obtaining scat for diet estimation and sampling diverse bear behaviours across a range of cluster durations. To avoid disturbing bears, I visited clusters 41 ± 15 days after the first fix in the cluster.

Once crews located bear scat at a cluster, approximately 50 mL were collected. To avoid pseudoreplication in dietary inferences because of oversampling scats from the same bear, or collecting more scats at locations where bears had spent longer time (ungulate carcasses), only one scat per site was collected for diet analysis (Bacon et al. 2011). Only scats for which estimated age matched the date when the bear was present at the site were collected (Wasser et al. 2004). If multiple scats were present at a site and all appeared of the same relative freshness, one scat was sampled randomly.

Thirty mL of each sample were autoclaved and rinsed through a 0.5 mm metal sieve to remove small soil and sand particles. Samples were air dried overnight in a fume hood and transferred to wide diameter petri dishes of one standard size. The sample was spread flat over the dish and a dissecting microscope grouped roots, herbaceous material, berries, ungulates, small mammals, insects, and miscellaneous (e.g., soil, rock, wood). A grid of 2×2-cm squares was placed below the dish and used to estimate the percentage of each broad food item relative to total fecal sample excluding miscellaneous material. This technique allowed estimation of proportion of various food items in scat for the same standardized sample volume (Schwab et al. 2011).

I identified species consumed by bears whenever possible, by taking up to 20 subitems (mode 20) for each broad food item per scat sample. I applied this procedure for herbaceous material fragments, berries, mammalian hairs and insects. All roots were assumed to be *Hedysarum* spp. (Munro et al. 2006). Herbaceous samples were assessed based on leaf morphology (i.e., lamina, apex and base shape, margin, gland position) and epidermal characteristics (i.e., stomatal complex and trichomes) (Dilcher 1974, Riegert and Singh 1982). Berries were identified based on morphological differences of seeds (i.e., size, aspect, colour, surface aspect). For herbaceous material and berries, I collected samples in the study area and created seed and herbaceous reference collections as well as microscopy slides based on foods consumed by bears in western Canada (Nielsen et al. 2003, Munro et al. 2006) to which I added *Melilotus* spp. planted on reclaimed mines. All vegetation were validated against three reference collections (University of Alberta Herbarium, Edmonton, Alberta; Foothills Research Institute Grizzly Bear Program, Hinton, Alberta; my own seed and herbaceous collection of bear foods). Mammals were identified to species based on hair medulla and scales/cuticula identification (Moore et al. 1974, Teerink 1991, Jones et al. 2009). Insects were classified into Formicidae (ants) and Coleoptera (beetles).

GPS Cluster Feeding Assessment

Crews meticulously searched cluster sites for any evidence of bear feeding on animal and plant matter following a similar protocol to Munro et al. (2006). Feeding sign in a 20×20-m plot centred on the most time consuming bear activity encountered was recorded, where ungulate consumption was the lengthiest activity, followed by bedding, and vegetation feeding.

Typical sites where bears had fed on animal prey included ungulate skeletal and hair remains, evidence of small mammal feeding such as diggings or displaced rocks and logs, or evidence of ant feeding such as split logs and excavated ant hills. Assigning mammalian prey to species was based on field evidence validated by laboratory microscopic identification of hair collected at kill sites as described in the 'Scat collection and analysis' section. Sign of feeding on plant material included evidence of digging for *Hedysarum* spp. roots, foraging on berries and grazing on graminoids and forbs. With the exception of graminoids, I differentiated herbaceous and berry material by species based on identification keys (Johnson et al. 1995, Kershaw et al. 1998) and when necessary by laboratory keying of plant samples collected in field. I separated forbs into native and non-native (introduced) based on USDA (2012).

Some cluster sites were assigned multiple foraging activities and for all sites I assigned activity by taking into account age of sign such as algal growth on carcass bones, plant growth inside root digs or greenness of grazed vegetation. For cluster with long duration, presence of specific food items in bear scat found at the site also was used to confirm feeding site assessments.

Frequency of Occurrence

I summarized total number of food items classed into categories sampled from cluster visitation and scat analysis (Table 4.1), and calculated frequency of occurrence of each item relative to total items and to total number of scats, respectively. Categories included plant (herbaceous, berry, root) and animal matter (ungulate, small mammal, bird, insect) matter, and detailed items were classified to species, genus or family level depending on my ability to identify subitems. For scat sampling, I also calculated frequency of occurrence for each taxonomically identifiable subitem relative to total number of subitems.

Biomass Estimation

To estimate biomass ingested based on scat analysis I used published correction factors from captive bear feeding trials (Hewitt and Robbins 1996). Scat biomass estimates for ungulates are sensitive to proportion of hair ingested by bears which affects correction factors. I followed Dahle et al. (1998) and modified the Hewitt and Robbins (1996) correction factors based on field evidence of hair ingestion and kill/scavenge data from GPS clusters (Table S.1).

I used bear behaviour sign, time bear spent at a cluster site based on GPS cluster information, and maximum daily intake rates for bears of different body sizes to estimate dry biomass ingested at each site. Intake rates were taken from the literature on bears in captive trials feeding on ungulates (Mattson 1997), small mammals (Pritchard and Robbins 1990, Berkes et al. 1994), birds (Bissett 1974), insects (Brian 1978), roots (Hamer 1999), herbaceous material (Rode et al. 2001), and berries (Welch et al. 1997). Whenever available, species-specific food item estimates were used. For ungulates, estimates were sex and age-specific based on mean body sizes in Alberta (Knopff et al. 2010), and were corrected for skeletal, rumen and water weights (Mattson 1997). If the bear had not bedded at the site, I assumed that it spent the entire time engaged in foraging, therefore biomass calculations reflected the entire cluster duration. For sites where bears spent long periods, primarily at ungulate carcasses, I assumed that bears fed on the ungulate for 16 h in every 24-h cycle, based on known bedding duration for the sampled bears (7.7 ± 4.7 h).

Food Availability

To assess food availability for foothills, mountains and reclaimed mines I estimated percentage cover of major grizzly bear plant foods (herbaceous, roots, berries) and performed ungulate pellet counts in the 20×20-m field plots also used for recording bear activity sign ($n_{foothills} = 494$; $n_{mountains} = 225$; $n_{reclaimed\ mines} = 166$). These plots included a 50:50 ratio of sites used by radiocollared bears during my study and random sites 300 m away from used sites. All of the landscape, except steep rock and water bodies, was available to bears and used and random sites were included to characterize foods by land designation. The presence of plant foods was assessed in five 0.7×0.7-m quadrants equally spaced on a north-south transect through the centre of each plot. If this direction followed a stream or trail, transects were shifted to east-west to minimize spatial autocorrelation in species composition between quadrants. With the exception of graminoids, herbaceous foods were identified to species level and categorized into native or non-native. In addition, I performed an inventory of herbaceous species in the same quadrants to estimate species richness by land designation. To avoid misrepresentation of availability based on phenology and detection error, I converted all cover estimates and counts to presence/absence of food items in the plots. Presence of ungulates was primarily recorded based on occurrence of fecal pellets, and in 16.7% of cases when snow covered >25% of the plot, with the aid of foot tracks in the snow. I considered deer (*Odocoileus* spp.) and bighorn sheep (*Ovis canadensis*) together because I was unable to reliably distinguish the pellets of these two species.

Statistical Analyses

For both scat analysis and GPS location cluster visitation, I used contingency table chi-square analyses to assess differences in food composition between foothills, mountains and reclaimed mines. In the case of the GPS cluster method I did not include berries, small mammals and insects in statistical analyses because of small sample sizes. Birds were omitted from all analyses also because of low sample sizes.

I used generalized linear models (GLMs) to investigate differences in proportion occurrence of each food item in scat between land designations, with location (land designation) as predictor variable. I set location on reclaimed mines as the base of comparison with foothill and mountain areas. Proportion of occurrence of a specific food type as dependent variable was rescaled to 0 and 1 to enable fitting of a logistic model (http://www.ats.ucla.edu/stat/stata /faq/proportion.htm) in STATA v.11.2 (StataCorp, College Station, Texas). I used a similar approach to assess differences in proportion biomass estimated to have been ingested by land designation, performing separate GLMs for the scat and GPS methods and for each food item. Robust standard errors were calculated in STATA to account for potential misspecification of the probability distribution family. I assessed model fit by inspecting deviance residuals to identify potential outliers or influential observations. In addition, I computed predicted values from the model output and calculated the correlation with observed values of the dependent variable. High correlations were considered indicative of good predictive power (Zheng and Agresti 2000).

To assess food availability, I used logistic regression with robust standard errors to estimate whether certain food items as quantified with my 20×20-m plot data were more likely to be present on the landscape on specific land designations. I assessed whether models were statistically significant using Wald chi-square tests. Link tests were computed to check for specification error with regard to location being a relevant predictor. Pregibon leverage values (Pregibon 1981) were calculated and plotted against predicted probabilities of occurrence to detect potential influential observations. Differences in herbaceous species richness between land designations were assessed using two-sample Wilcoxon rank-sum tests.

RESULTS

Overall Patterns

Grizzly bears foraged in the foothills, mountains, and on reclaimed mines. Of the 445 location clusters visited, I found evidence of bear feeding at 234 clusters (52.6%). The majority of clusters (91.5%) had only one type of bear feeding activity, with some clusters having two types of feeding (8.5%). This method resulted in 23 plant and animal species/genera consumed by bears, including 5 berry, 12 herbaceous, 1 root, 5 ungulates, as well as 7 taxonomic groups encompassing 1 plant, 4 small mammals, 1 bird and 1 insect (Table S.2). Overall, the top three occurring food items consumed by bears and located via cluster visitation were *Hedysarum* spp. roots (22.2%), elk (11.3%) and deer (10.2%).

I collected and analyzed 331 scat samples, found 866 broad food items and selected 6,877 subitems for taxonomical identification. Only 20.9% of scats had a single food item, with most scats (90.3%) having 1-4 items (331 scats; range 1−7). I identified 32 species/genera, including 14 berry, 6 herbaceous, 1 root, 5 ungulate, 6 small mammal, along with 5 taxonomic groups comprised of 1 plant, 2 small mammal and 2 insect (Table S.2). Similar to cluster data, the principal items occurring in bear scat was *Hedysarum* spp. roots (21.5%). However, the second and third most common items in scat were represented by plant, not animal matter: graminoids (19.4% of items; 25.1% of subitems) and clovers, *Trifolium/Melilotus* spp. (15.6% of items; 17.3% of subitems).

Deviance residuals for GLMs plotted against unique id-s of sites visited during GPS cluster sampling/scat collection generally did not reveal any major outliers or influential observations. However, berry, small mammal and insect models had higher deviances compared to herbaceous, root and ungulate models, suggesting better fits for the latter three food items. Correlations between predicted and observed values of the dependent variable also showed that herbaceous, root and ungulate models had best fit. This pattern held for both diet analysis methods (Table 4.2).

Frequency of Occurrence (Scat analysis & GPS clusters)

I found significant differences in diet estimation between scat and GPS methods (χ^2 = 149.58, *df* = 5, $P < 0.0001$). These differences were chiefly caused by high presence of ungulate items at clusters (42%) compared to scat samples (11%) and increased occurrence of non-ungulate items in scat (small mammals 9%; insects 5%; berries 7%) compared to clusters (small mammals 3%; insects 2%; berries 2%). Despite this variability, both methods showed that grizzly bear diet composition differed between foothills and mountains (Scat χ^2 = 32.43, *df* = 5, $P < 0.0001$; GPS χ^2 = 42.04, *df* = 5, $P < 0.0001$), foothills and reclaimed mines (Scat χ^2 = 36.72, *df* = 5, $P < 0.0001$; GPS χ^2 = 84.97, *df* = 5, $P < 0.0001$) and mountains and reclaimed mines (Scat χ^2 = 45.88, *df* = 5, $P < 0.0001$; GPS χ^2 = 81.45, *df* = 5, $P < 0.0001$).

Animal matter was consumed most frequently by bears in the foothills (Scat 31.3%; GPS 64.2%), with plant material also occurring in the diet (Scat 68.7%; GPS 35.8%). The opposite results of the two methods for the foothills region are largely due to high occurrence of moose (*Alces alces*) at GPS clusters (33% of species-assigned ungulate carcasses) and low moose occurrence in scat samples (8% of scats containing ungulate hair). Animal matter was consumed less frequently in the mountains (Scat 19.5%; GPS 35.3%), where plants predominated (Scat 80.5%; GPS 64.7%). Finally, animal material was least present in bear diet on reclaimed mines (Scat 12.8%; GPS 19.7%), where vegetative feeding was most prevalent (Scat 87.2%; GPS 80.3%).

In the foothills and on reclaimed mines, ungulates were the most frequent animals to occur in bear diet (Table 4.1). Elk, moose and deer were most frequent in the foothills whereas deer, bighorn sheep and elk were most frequent on reclaimed mined. However, elk were significantly less likely to occur in diet on mines compared to the foothills (Table 4.2). Based on the GPS method, when compared to reclaimed mines, elk occurred more frequently in bear diet in the mountains, whereas deer occurred less often. Scat analysis showed an increased frequency of small mammal consumption outside mines compared to mines, accounted for primarily by ground squirrels (Sciuridae). Insects in scat were almost exclusively Formicidae, and birds (Tetraoninae) were detected at two GPS location clusters but were absent in scat.

Plant matter occurrence in bear diet also differed by land designation. In the foothills, based on both methods herbaceous feeding occurred most frequently, with the main plants consumed being graminoids, *Trifolium/Melilotus* spp. and *Equisetum* spp. Feeding on *Heracleum lanatum* was infrequent. In the mountains, *Hedysarum* spp. roots were the most frequent food item based on the GPS method, whereas scat analysis found comparable occurrence of root and herbaceous material. Herbaceous species composition was relatively similar between mountains and foothills. On reclaimed mines, both methods showed high occurrence of herbaceous material compared to all other food items, primarily because of graminoids, *Trifolium/Melilotus* spp., *Equisetum* spp. and *Medicago* spp., the latter being the dominant plant group at location clusters on reclaimed mines (33%). Berries, mainly *Shepherdia canadensis*, *Empetrum nigrum* and *Vaccinium scoparium* occurred in low proportion in bear diet (Scat 6.9%; GPS 2%).

Biomass Estimation (Scat analysis & GPS clusters)

Biomass estimated to have been ingested by bears varied in the foothills, mountains and on reclaimed mines (Figure 4.2). There was a predominance of ungulate biomass in the foothills (95.1%) compared to the other land designations (Table 4.3). Herbaceous biomass consumed was highest on reclaimed mines (42%), whereas roots were the main source of biomass in the mountains (47.9%)

and were consumed significantly more outside mines. This differential dominance of various food items by land designation was statistically significant (Table 4.3).

Moose and elk contributed significantly more to total biomass consumed by bears in the foothills than in the mountains (Table 4.3, Figure 4.3). On reclaimed mines, most biomass came from deer (Scat 16.2%; GPS 27.5%), elk (Scat 2.8%; GPS 22%) and bighorn sheep (Scat 6.2%; GPS 6.9%).

Graminoids and native and non-native forbs were present in the diets of bears on all land designations, but contributed differently to estimated ingested biomass (Figure 4.4). On reclaimed mines, both methods showed that bears consumed disproportionately more biomass of non-native plants compared to any other herbaceous material and this plant biomass contributed significantly more to total biomass on reclaimed mines than outside the mines (Table 4.3, Figure 4.4).

Biomass estimation for berry, small mammal and insect foods must be treated with caution due to lower model fits (Table 4.3). These items accounted for smaller amounts in the biomass estimates: small mammals (Scat 10.8%; GPS <1%); berries (Scat 6.3%; GPS <1%); insects (Scat 1.7%; GPS <1%). A full taxonomical listing of foods and their biomass contributions are provided in Table S.3.

Food Availability

With the exception of marginal significance for the graminoid model, all models predicting probability of food presence were significant at $\alpha = 0.05$ level (Table 4.4). Location was a particularly relevant predictor for half of the food occurrence models ($P_{hat} < 0.05$), specifically berry, native forb, non-native forb and deer/bighorn sheep models. Bear foods most likely to be present on reclaimed mines included non-native forbs, deer/bighorn, and elk.

As anticipated, reclaimed mines had considerably lower herbaceous species richness (5.3 ± 3.8 species) than foothills (8.9 ± 4.8 species) and mountains (8.2 ± 4.1 species). Differences in richness were statistically significant for mines compared to foothills (two-sample Wilcoxon rank-sum, $z = -8.65$, $df_1 = 166$, $df_2 =$

494, $P < 0.0001$), mines compared to mountains (two-sample Wilcoxon rank-sum, $z = -6.96$, $df_1 = 166$, $df_2 = 225$, $P < 0.0001$) but not for foothills and mountains (two-sample Wilcoxon rank-sum, $z = 1.31$, $df_1 = 494$, $df_2 = 225$, $P = 0.19$).

DISCUSSION

I describe the diet of grizzly bears on reclaimed open-pit mines, comparing it to undisturbed landscapes outside mines. I discuss bear food habits in relation to food availability and in connection to historical data before extensive reclamation occurred in the region. Mine reclamation in the otherwise predominantly forested foothills and mountains resulted in habitat openness, dominance of non-native vegetation, and low plant species richness. Reclaimed mines support large ungulate populations likely because of forage sown as part of reclamation (BWT 2010). Some species, particularly elk and bighorn sheep are more available on than outside mines. However, mines also might serve as refugia from predators because high visibility in open habitats allows early predator detection (Kie 1999, Ripple and Beschta 2004).

I demonstrated that grizzly bears in an industrially modified landscape consume non-native forbs which, along with graminoids and to a much lower extent native plants, make up the largest (Scat) or second largest (GPS) percentage of dry biomass estimated to have been ingested by bears on reclaimed mines. Munro et al. (2006) also found graminoids and *Trifolium* spp. to be an important part of bear diet in the region six years before my work. However, particularly for mined sites I found more non-native herbaceous plants in diet compared to native forbs (*Heracleum lanatum* and *Lathyrus ochroleucus*) that were important in their study. Non-native herbaceous foods are concentrated on mines attracting bears, but most herbaceous material loses nutritional value in the fall (Morgantini and Hudson 1989, Alldredge et al. 2002, Wagner and Peek 2006). Correspondingly, during fall bears move primarily outside mines where they feed on berries, ungulates and roots in preparation for winter denning (Cristescu et al. 2011).

Hedysarum spp. roots are a key grizzly bear food in the Rocky Mountains (Zager and Jonkel 1983, Weaver et al. 1996) and similarly to Munro et al. (2006), I found that roots were the primary bear food in the mountains, where they are present in highest availability. Berries are an important energy source for grizzly bears in preparation for winter denning (Weaver et al. 1996, Welch et al. 1997) and berry consumption in my study occurred primarily in the mountains and foothills, with least consumption on mines. This pattern coincides with low berry availability on mines compared with the surrounding landscape.

A high proportion of meat in bear diet results in body mass gain and is associated with increased reproductive success (Hilderbrand et al. 1999). Similar to Munro et al. (2006), 2009-2010 diet in the foothills was dominated by ungulates. Based on 54 field visited ungulate carcasses, Munro et al. (2006) identified moose as the main ungulate consumed by bears (83%), followed by deer (16%) and elk (1%), but did not detect bighorn sheep in bear diet. Based on larger sample sizes and the addition of scat analysis, I demonstrated differences in ungulate consumption by land designation. Ungulates were consumed in the lowest biomass on reclaimed mines, although my data and an independent survey showed high presence of bighorn sheep and mule deer on the larger reclaimed mine in my study area (BWT 2010). Because bears consumed more deer than bighorn sheep biomass but deer were present in lower numbers (BWT 2010), I can conclude that bears selected for deer on mines. Bighorn sheep use of open habitats with high visibility combined with flocking behaviour and presence of escape terrain (Risenhoover and Bailey 1985) renders this species less vulnerable to predation on reclaimed mines than the more solitary deer which cannot access the artificial escape terrain designed for bighorn sheep as part of reclamation.

Perhaps the most noteworthy difference in 2009-2010 ungulate diet compared to 2001-2003 was the substantial increase in elk consumption by bears on all land designations. Although elk are most available on mines compared with outside mines, large group sizes, vigilance and ease of predator detection in open grasslands (Hebblewhite et al. 2005) characteristic of mines make elk difficult to capture. Similar to deer and bigorn sheep, elk numbers on the largest reclaimed mine in the study area increased following reclamation (BWT 2010). Outside mines, bears select elk more than expected from availability. Based on field evidence at GPS clusters, scavenging on cougar and wolf kills is an important meat acquisition strategy by grizzly bears (Chapter 5).

While reclaimed mines provide feeding opportunities for grizzly bears, moose dominated bear diet in the foothills. In contrast, reclaimed mines had the lowest moose availability likely due to rarity of moose browsing material, and I found no evidence of bears feeding on moose on mines.

GPS cluster visitation is useful for assessing the diet of obligate predators feeding on large prey that take a long time to consume (Merrill et al. 2010). For such predators, the GPS method underestimates the dietary frequency of small prey, but does not skew estimates of the biomass composition of prey, which are chiefly driven by large prey (Bacon et al. 2011). In the case of complex diets, such as for facultative carnivores/omnivores, I have herein shown that the GPS method largely overestimates the proportion of ungulates in diet because clusters form by definition during feeding on items that take long time to consume, i.e., ungulate carcasses. Inferences on non-ungulate food consumption based on the GPS cluster method should be treated with caution and researchers should be aware that any method of diet estimation has associated biases (Klare et al. 2011).

A potential bias in estimating prey composition from scat comes from scat collection at preferential feeding sites. While sampling scat randomly avoids such bias, collection of scat encountered along transects, trails or roads produces lower sample sizes and does not allow inferences on habitat features associated with the actual feeding site. Sampling along linear features may raise other biases, such as over-representation of herbaceous material grazed by bears on road right-of-ways, or under sampling from individuals that avoid trails or roads. Walking transects with scat detection dogs could minimize such biases. In addition, gut retention might have affected scat analysis by land designation, with some scats collected on mines possibly reflecting bear diet in the vicinity of mines. I do not consider this a serious concern because bears often spent several weeks at a time on mines foraging and resting.

Scats can be collected non-invasively without the need for animal capture, but require extensive effort for food item identification in the lab, and scat analysis does not render date, time, or location of feeding activity. In contrast, while extremely costly and field intensive compared to scat analysis, cluster visitation provides additional opportunities for collection of habitat data at feeding localities, comparisons with similar data recorded at random locations to assess feeding site selection, and the advantage of assigning ungulate consumption to predation or scavenging. If the goal is to understand predator-prey dynamics, then underestimation of scavenging produces inflated predation estimates while undervaluing indirect consumptive effects (Wilson & Wolkovich 2011).

For optimal description of composition and biomass of complex obligate and facultative carnivore diets I recommend scat analysis in conjunction with GPS cluster visitation. Cluster visitation becomes particularly important in the case of diets with high proportion of meat, such as grizzly bears in my study system. Cluster investigations can be used to refine scat analysis, such as through improved estimation of prey biomass by incorporating prey sex and age recorded during cluster visitation. This information is unavailable from hair in scat. In addition, cluster visitation allows estimation on percentage of hair ingested by the predator and thus informed correction factors for meat consumption. Without field knowledge of amount of hair consumed, estimates of meat biomass ingested by grizzly bears can vary 15-fold (Hewitt and Robbins 1996).

Although Simberloff (1999) cautioned against considering the grizzly bear as a keystone species, berry seed dispersal, soil aeration through root digging (Tardiff and Stanford 1998), and movement of nitrogen from marine to terrestrial ecosystems through salmon consumption (Gende et al. 2002) are examples where grizzly bears had large effects on the environment. In contrast, my data on grizzly bear foraging on non-native forbs in industrially disturbed landscapes cautions against viewing this species as a keystone element in wilderness ecosystems.

Grizzly bears are likely the least resilient of all Rocky Mountains large carnivores (Weaver et al. 1996), but my results suggest that this species can adapt to exploit novel habitats created through reclamation. Despite this behavioural ability to adapt to change, persistence of bears is linked to availability of seasonal food sources and their presence on the landscape occurs in the context of large wilderness areas. In my study system, herbaceous foods artificially introduced on reclaimed mine sites attract bears from the surrounding wild landscape. Planting berries and *Hedysarum* spp. as part of reclamation may encourage use of mines in all seasons. However, concentrating bear foods might have negative repercussions if it were to result in infanticide by male bears (Ben-David et al. 2004), or if it were to increase the risk of illegal shooting on these predominantly open landscapes. These considerations highlight the need for land-use planning and access management that incorporate protection of reclaimed mines following mine closure. Substantial consumption of non-native plants and ungulates that I documented calls for including these foods into planning schemes designed to minimize risk of grizzly bear conflict with people.

I conclude that grizzly bears have adapted their feeding patterns to an industrially reclaimed landscape by switching their diet to exploit novel availability of foods. By consuming ungulates and herbaceous material on mines, bears have become an integral part of ecosystem succession for this particular type of industrial disturbance. Although concerns over the consequences of industrial development are legitimate, in Alberta rampant road development and slow response by the province to confront access management are major issues hindering grizzly bear conservation. Reclaimed mines can provide food resources to grizzly bears, and decreasing direct mortality from shooting bears along human access features is key to population persistence, possibly making the difference between reclaimed areas being sources or sinks (Nielsen et al. 2006).

LITERATURE CITED

Alldredge, M. W., J. M. Peek, and W. A. Wall. 2002. Nutritional quality of forages used by elk in Northern Idaho. Journal of Range Management **55**:253-259.

Bacon, M. M., G. M. Becic, M. T. Epp, and M. S. Boyce. 2011. Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. Wildlife Society Bulletin **35**:409-415

Ballard, W. B., S. D. Miller, and J. S. Whitman. 1990. Brown and black bear predation on moose in southcentral Alaska. Alces **26**:1-8.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs **169**:1-30.

Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? Oecologia **138**:465-474.

Berkes, F., P. J. George, R. J. Preston, A. Hughes, J. Turner, and B. D. Cummins. 1994. Wildlife harvesting and sustainable regional native economy in the Hudson and James Bay Lowland, Ontario. Arctic **47**:350-360.

Bissett, D. 1974. Resource harvests - hunter-trappers in the Mackenzie Valley (economic and social significance). Environmental-Social Committee, Task Force on Northern Oil Development. Report 74-42. 208pp.

Boulanger, J., G. B. Stenhouse, M. Proctor, S. Himmer, D. Paetkau, and J. Cranston. 2005. 2004 Population inventory and density estimates for the Alberta 3B and 4B Grizzly bear management area. Report prepared for Alberta Sustainable Resource Development, Fish and Wildlife Division. Integrated Ecological Research, Nelson, BC, Canada.

Brian, M. V. 1978. Production ecology of ants and termites. Cambridge University Press, Cambridge, UK.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and

C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology **16**:909-923.

BWT. 2010. Cheviot and Luscar mine Wildlife Inventory 2009. Created for Teck Coal Limited, Cardinal River Operations, by Bighorn Wildlife Technologies Ltd., Hinton, AB, Canada.

Cameron, A. R., and G. G. Smith. 1991. Coals of Canada: Distribution and compositional characteristics. International Journal of Coal Geology **19**:9-20.

Cattet, M., J. Boulanger, G. Stenhouse, R. A. Powell, and M. L. Reynolds-Hogland. 2008. An evaluation of long-term capture effects in ursids: Implications for wildlife welfare and research. Journal of Mammalogy **89**:973-990.

Choi, Y. D., V. M. Temperton, E. B. Allen, A. P. Grootjans, M. Halassy, R. J. Hobbs, M. A. Naeth, and K. Torok. 2008. Ecological restoration for future sustainability in a changing environment. Ecoscience **15**:53-64.

Colinvaux, P. 1979. Why big fierce animals are rare: an ecologist's perspective. Princeton University Press, Princeton, USA.

Cristescu, B., G. B. Stenhouse, M. Symbaluk, and M. S. Boyce. 2011. Land-use planning following resource extraction – Lessons from grizzly bears at reclaimed and active open-pit mines. In eds. A.B. Fourie, M. Tibbett, and A. Beersing: Mine Closure 2011, Proceedings of the Sixth International Conference on Mine Closure. Australian Centre for Geomechanics, Nedlands, Australia.

Cristescu, R. H., C. l. Frere, and P. B. Banks. 2012. A review of fauna in mine rehabilitation in Australia: Current state and future directions. Biological Conservation **149**:60-72.

Dahle, B., O. J. Sorensen, E. H. Wedul, J. E. Swenson, and F. Sandegren. 1998. The diet of brown bears *Ursus arctos* in central Scandinavia: Effect of access to free-ranging domestic sheep *Ovis aries*. Wildlife Biology **4**:147-158.

Dall, S. R. X., and R. A. Johnstone. 2002. Managing uncertainty: information and insurance under the risk of starvation. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences **357**:1519-1526.

Dall, S. R. X., L. A. Giraldeau, O. Olsson, J. M. McNamara, and D. W. Stephens. 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology and Evolution **20**:187-193.

DeFries, R. S., J. A. Foley, and G. P. Asner. 2004. Land-use choices: balancing human needs and ecosystem function. Frontiers in Ecology and the Environment **2**:249-257.

del Moral, R., L. R. Walker, and J. P. Bakker. 2007. Insights gained from succession for the restoration of landscape structure and function. In eds. L. R. Walker, J. Walker, and R. J. Hobbs: Linking restoration and ecological succession. Springer, New York, USA.

Dilcher, D. L. 1974. Approaches to identification of Angiosperm leaf remains. Botanical Review **40**:1-157.

Ehrlich, P. R., G. Wolff, G. C. Daily, J. B. Hughes, S. Daily, M. Dalton, and L. Goulder. 1999. Knowledge and the environment. Ecological Economics **30**:267-284.

Erickson, D. L. 1995. Policies for the planning and reclamation of coal-mined landscapes: An international comparison. Journal of Environmental Planning and Management **38**:453-467.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soule, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of Planet Earth. Science **333**:301-306.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics **34**:487-515.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science **309**:570-574.

Frank, D. A. 1998. Ungulate regulation of ecosystem processes in Yellowstone National Park: Direct and feedback effects. Wildlife Society Bulletin **26**:410-418.

Fretwell, S. D. 1987. Food chain dynamics: The central theory of ecology? Oikos **50**:291-301.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience **52**:917-928.

Hamer, D. 1999. Forest fire's influence on yellow hedysarum habitat and its use by grizzly bears in Banff National Park, Alberta. Canadian Journal of Zoology **77**:1513-1520.

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

Hewitt, D. G., and C. T. Robbins. 1996. Estimating grizzly bear food habits from fecal analysis. Wildlife Society Bulletin **24**:547-550.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology **77**:132-138.

Hobbs, R. J., and J. A. Harris. 2001. Restoration ecology: Repairing the Earth's ecosystems in the New Millennium. Restoration Ecology **9**:239-246.

Holl, K. D. 2002. Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. Journal of Applied Ecology **39**:960-970.

Houghton, R. A. 1994. The worldwide extent of land-use change. BioScience **44**:305-313.

Jansen, B. D., P. R. Krausman, K. D. Bristow, J. R. Heffelfinger, and J. C. deVos, Jr. 2009. Surface mining and ecology of desert bighorn sheep. Southwestern Naturalist **54**:430-438.

Johnson, D., L. Kershaw, A. MacKinnon, and J. Pojar. 1995. Plants of the western boreal forest and aspen parkland. Lone Pine Publishing, Vancouver, BC, Canada.

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

Jones, P., S. Sfez, P. Knamiller, and E. Merrill. 2009. Mammalian hair key with special reference to adult and juvenile ungulates on the Eastern slopes of the Canadian Rocky Mountains. University of Alberta, Edmonton, AB, Canada.

Karmacharya, S., M. Symbaluk, D. Brand, and S. Schwartz. 2011. Life of coal mine planning - engaging in land use planning at Luscar and Gregg River Mines. In eds. A.B. Fourie, M. Tibbett, and A. Beersing: Mine Closure 2011 — Proceedings of the Sixth International Conference on Mine Closure. Australian Centre for Geomechanics, Nedlands, Australia.

Kennedy, C. 2002. Alternatives for the reclamation of surface mined lands. In eds. A. Mudroch, U. Stottmeister, C. Kennedy, and H. Klapper: Remediation of abandoned surface coal mining sites: a NATO-Project. Springer, Berlin, Germany.

Kershaw, L., A. MacKinnon, and J. Pojar. 1998. Plants of the Rocky Mountains. Lone Pine Publishing, Vancouver, BC, Canada.

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

Klare, U., J. F. Kamler, and D. W. Macdonald. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. Mammal Review **41**:294-312.

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.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management **74**:1435-1447.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience **54**:123-138.

Larkin, J. L., D. S. Maehr, J. J. Krupa, J. J. Cox, K. Alexy, D. E. Unger, and C. Barton. 2008. Small mammal response to vegetation and spoil conditions on a reclaimed surface mine in Eastern Kentucky. Southeastern Naturalist **7**:401-412.

Larsen, D., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortaility in southwest Yukon. Journal of Wildlife Management **53**:548-557.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears - *Ursus arctos*. Biological Conservation **81**:161-177.

Mattson, D. J., and T. Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850 –2000. Conservation Biology **16**:1123-1136.

McCoy, E. D., and H. R. Mushinsky. 2002. Measuring the success of wildlife community restoration. Ecological Applications **12**:1861-1871.

McDonald, L. L. 2004. Sampling rare populations. In ed. W.L. Thompson: Sampling rare or elusive species. Island Press, Washington, USA.

Merrill, E., H. k. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair. 2010. Building a mechanistic understanding of predation with GPS-based movement data. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2279-2288.

MiHR. 2010. Canadian mining industry employment and hiring forecasts. HR Forecasts, Mining Industry Human Resources Council, Kanata, ON, Canada.

Moore, T. D., L. E. Spence, and C. E. Dugnolle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game Fish Department, Bulletin No. 14: 1-177.

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

Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy **87**:1112-1121.

Mysterud, A. 2006. The concept of overgrazing and its role in management of large herbivores. Wildlife Biology **12**:129-141.

Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience **10**:1-10.

Nielsen, S. E., S. Herrero, M. S. Boyce, R. D. Mace, B. Benn, M. L. Gibeau, and S. Jevons. 2004. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biological Conservation **120**:101-113.

Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation **130**:217-229.

Paschke, M. W., E. F. Redente, and S. L. Brown. 2003. Biology and establishment of mountain shrubs on mining disturbances in the Rocky Mountains, USA. Land Degradation & Development **14**:459-480.

Pregibon, D. 1981. Logistic regression diagnostics. Annals of Statistics **9**:705-724.

Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology **68**:1645-1651.

Proctor, M. F., D. Paetkau, B. N. McLellan, G. B. Stenhouse, K. C. Kendall, R. D. Mace, W. F. Kasworm, C. Servheen, C. L. Lausen, M. L. Gibeau, W. L. Wakkinen, M. A. Haroldson, G. Mowat, C. D. Apps, L. M. Ciarniello, R. M. R. Barclay, M. S. Boyce, C. C. Schwartz, and C. Strobeck. 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. Wildlife Monographs **180**:1-46.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. The Quarterly Review of Biology **52**:137-154.

Riegert, P. W., and N. Singh. 1982. A key to identify epidermal fragments of Saskatchewan rangeland plants. Canadian Journal of Botany **60**:2461-2468.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? BioScience **54**:755-766.

Risenhoover, K. L., and J. A. Bailey. 1985. Foraging ecology of mountain sheep: Implications for habitat management. Journal of Wildlife Management **49**:797-804.

Rode, K. D., C. T. Robbins, and L. A. Shipley. 2001. Constraints on herbivory by grizzly bears. Oecologia **128**:62-71.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics **2**:369-404.

Schwab, C., B. Cristescu, M. S. Boyce, G. B. Stenhouse, and M. Ganzle. 2009. Bacterial populations and metabolites in the feces of free roaming and captive grizzly bears. Canadian Journal of Microbiology **55**:1335-1346.

Schwab, C., B. Cristescu, J. M. Northrup, G. B. Stenhouse, and M. Ganzle. 2011. Diet and environment shape fecal bacterial microbiota composition and enteric pathogen load of grizzly bears. PLoS ONE **6**:e27905.

Scott, T. A., W. Wehtje, and M. Wehtje. 2001. The need for strategic planning in passive restoration of wildlife populations. Restoration Ecology **9**:262-271.

Sergio, F., T. Caro, D. Brown, B. Clucas, J. Hunter, J. Ketchum, K. McHugh, and F. Hiraldo. 2008. Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. Annual Review of Ecology Evolution and Systematics **39**:1-19.

Simberloff, D. 1999. Biodiversity and bears: A conservation paradigm shift. Ursus **11**:21-27.

Smyth, C. R. 1997. Early succession patterns with a native species seed mix on amended and unamended coal mine spoil in the Rocky Mountains of Southeastern British Columbia, Canada. Arctic and Alpine Research **29**:184-195.

Soule, M. E., J. A. Estes, J. Berger, and C. M. Del Rio. 2003. Ecological effectiveness: Conservation goals for interactive species. Conservation Biology **17**:1238-1250.

Stephens, D. W., and J. R. Krebs. 1987. Foraging Theory. Princeton University Press, Princeton, USA.

Stephens, D. W., J. S. Brown, and R. C. Ydenberg. 2007. Foraging: behavior and ecology. University of Chicago Press, Chicago, USA.

Tardiff, S. E., and J. A. Stanford. 1998. Grizzly bear digging: Effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology **79**:2219-2228.

Teerink, B. J. 1991. Hair of west-European mammals. Atlas and identification key. Cambridge University Press, Cambridge, UK.

USDA. 2012. The PLANTS Database. United States Department of Agriculture, Natural Resources Conservation Service, National Plant Data Team, Greensboro, NC, USA. online [URL]: http://plants.usda.gov, accessed 1 May 2012.

Venter, O., N. N. Brodeur, L. Nemiroff, B. Belland, I. J. Dolinsek, and J. W. A. Grant. 2006. Threats to endangered species in Canada. BioScience **56**:903-910.

Visconti, P., R. L. Pressey, D. Giorgini, L. Maiorano, M. Bakkenes, L. Boitani, R. Alkemade, A. Falcucci, F. Chiozza, and C. Rondinini. 2011. Future hotspots of terrestrial mammal loss. Philosophical Transactions of the Royal Society B: Biological Sciences **366**:2693-2702.

Wagner, G. D., and J. M. Peek. 2006. Bighorn sheep diet selection and forage quality in central Idaho. Northwest Science **80**:246-258.

Wasser, S. K., B. Davenport, E. R. Ramage, K. E. Hunt, M. Parker, C. Clarke, and G. Stenhouse. 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. Canadian Journal of Zoology **82**:475-492.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10**:964-976.

Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. Ecology **78**:1105-1119.

Wilson, E. E., and Wolkovich, E. M. 2011. Scavenging: how carnivores and carrion structure communities. Trends in Ecology and Evolution **26**:129-135.

World Energy Council. 2010. Survey of energy resources. London, UK.

Zager, P. E., and C. J. Jonkel. 1983. Managing grizzly bear habitat in the Northern Rocky Mountains. Journal of Forestry **81**:524-&.

Zheng, B. Y., and A. Agresti. 2000. Summarizing the predictive power of a generalized linear model. Statistics in Medicine **19**:1771-1781.

Zipper, C., J. Burger, J. Skousen, P. Angel, C. Barton, V. Davis, and J. Franklin. 2011. Restoring forests and associated ecosystem services on Appalachian coal surface mines. Environmental Management **47**:751-765.

Table 4.1: Grizzly bear diet composition in west-central Alberta, Canada, April−October 2009 and 2010. Diet was assessed based on scat analysis and feeding sign at GPS location clusters, and based on frequency of occurrence of food items relative to total items, total scats and taxonomically-identified total subitems.

Food category	Scat															GPS					
	Fth					Mt					Rmi					Fth		Mt		Rmi	
	#[a] 502	F[b] 502	F[c] 179	#[d] 4240	F[e] 4240	#[a] 200	F[b] 200	F[c] 91	#[d] 1333	F[e] 1333	#[a] 164	F[b] 164	F[c] 61	#[d] 1304	F[e] 1304	#[f] 165	F[g]	#[f] 65	F[g]	#[f] 71	F[g]
Plant																					
Herb	223	44.4	124.6	1535	36.2	73	36.5	80.2	559	41.9	116	70.7	190.2	940	72.1	30	18.2	6	9.2	57	80.3
Berry	35	7.0	19.6	399	9.4	18	9.0	19.8	247	18.5	7	4.3	11.5	51	3.9	3	1.8	3	4.6	0	0.00
Root	87	17.3	48.6	NA	NA	70	35.0	76.9	NA	NA	20	12.2	32.8	NA	NA	26	15.8	33	50.8	0	0.00
Animal																					
Ungulate	77	15.3	43.0	1276	30.1	13	6.5	14.3	208	15.6	9	5.5	14.8	133	10.2	98	59.4	16	24.6	13	18.3
Small mammal	51	10.2	28.5	522	12.3	17	8.5	18.7	138	10.4	6	3.7	9.8	80	6.1	6	3.6	3	4.6	0	0.00
Bird	0	0.0	0.0	0	0.0	0	0.0	0.0	0	0.0	0	0.0	0.0	0	0.0	1	0.6	1	1.5	0	0.00
Insect	29	5.8	16.2	508	12.0	9	4.5	9.9	181	13.6	6	3.7	9.8	100	7.7	1	0.6	3	4.6	1	1.4
Total	502	100.0	280.4	4240	100.0	200	100.0	219.8	1333	100.0	164	100.0	268.9	1304	100.0	165	100.0	65	100.0	71	100.0

[a] total number of items sampled from scats collected from foothills (Fth; *n* = 179), mountains (Mt; *n* = 91) and reclaimed mines (Rmi; *n* = 61). [b] % occurrence of items relative to total items. [c] % occurrence of items relative to total number of scats. [d] total number of taxonomically identifiable subitems in scat (i.e., total number of sampled berries, herbaceous fragments, ungulate/small hairs, bird feathers, and insects; roots were assumed to be *Hedysarum* spp.). [e] % occurrence of subitems relative to total number of subitems. [f] total number of items sampled from visitation of feeding clusters in the foothills (Fth; *n* = 136), mountains (Mt; *n* = 58) and reclaimed mines (Rmi; *n* = 40). [g] % occurrence of items relative to total items.

Table 4.2: Variation in estimated frequency of occurrence of food items from grizzly bear diet in west-central Alberta, Canada, April−October 2009 and 2010. Diet was assessed based on species-specific frequency of occurrence of foods available to bears from scat analyses and feeding sign at GPS location clusters. Reclaimed mines were withheld as the reference category in all models run.

Food category	**Scat**						**GPS**					
	Fth		**Mt**		**Model fit**[b]		**Fth**		**Mt**		**Model fit**[b]	
	β_i [a]	Robust SE	β_i [a]	Robust SE	Correlation coefficient	P_{corr}	β_i [a]	Robust SE	β_i [a]	Robust SE	Correlation coefficient	P_{corr}
Plant												
Berry	**1.02****	**0.50**	**1.28****	**0.53**	**0.11**	**<0.05**	14.83**	0.61	15.70**	0.62	0.11	0.11
Graminoid	**−0.73****	**0.17**	**−1.24****	**0.25**	**0.29**	**<0.05**	**−2.08****	**0.59**	**−3.19****	**1.07**	**0.31**	**<0.05**
Native forb	**−0.88****	**0.36**	**−1.03****	**0.46**	**0.16**	**<0.05**	0.53	0.63	−0.51	0.86	0.11	0.11
Non-native forb	**−1.11****	**0.19**	**−1.54****	**0.29**	**0.36**	**<0.05**	**−4.01****	**0.68**	**−3.86****	**1.05**	**0.62**	**<0.05**
Root	**0.51***	**0.30**	**1.62****	**0.32**	**0.35**	**<0.05**	**15.59****	**0.24**	**17.40****	**0.28**	**0.48**	**<0.05**
Animal												
Deer & Bighorn	**0.33**	0.50	−0.25	0.58	0.08	0.15	**−0.51**	**0.40**	**−1.51****	**0.58**	**0.18**	**<0.05**
Elk	**2.13****	**0.61**	**−0.03**	**0.82**	**0.25**	**<0.05**	**1.93****	**0.61**	**1.47****	**0.69**	**0.18**	**<0.05**
Moose	**16.32****	**0.45**	**NA**[d]	**NA**[d]	**0.11**	**<0.05**	**16.92****	**0.12**	**13.50****	**0.99**	**0.32**	**<0.05**
Small mammal	**1.14****	**0.50**	**0.97***	**0.55**	**0.12**	**<0.05**	14.91**	0.46	15.26**	0.61	0.10	0.14
Insect	0.46	0.46	0.88	0.54	0.07	0.20	−1.18	1.43	0.39	1.19	0.10	0.14

[a] coefficient estimated from GLM

[b] model fit assessed based on correlation between predicted values fitted via GLM and observed dependent variable values. Models with best fit ($\alpha = 0.05$) are in bold

[d] moose was not detected in scat samples collected in the mountains and on reclaimed mines

*significance at $\alpha = 0.05$ level ; **significance at $\alpha = 0.10$ level

Table 4.3: Variation in estimated biomass from grizzly bear diet in west-central Alberta, Canada, April−October 2009 and 2010. Diet was assessed based on species-specific biomass available to bears from scat analysis employing correction factors and feeding sign at GPS location clusters. Whenever possible, corrections incorporated season, age and sex of prey. Reclaimed mines were withheld as the reference category in all models run.

Food category	**Scat**						**GPS**					
	Fth		**Mt**		**Model fit**[b]		**Fth**		**Mt**		**Model fit**[b]	
	β_i[a]	Robust SE	β_i[a]	Robust SE	Correlation coefficient	P_{corr}	β_i[a]	Robust SE	β_i[a]	Robust SE	Correlation coefficient	P_{corr}
Plant												
Berry	1.18*	0.62	1.49**	0.66	0.10	0.06	15.38**	0.59	16.26**	0.60	0.11	0.10
Graminoid	**−0.53****	**0.23**	**−1.06****	**0.32**	**0.18**	**<0.05**	**−2.08****	**0.62**	**−2.68****	**1.07**	**0.29**	**<0.05**
Native forb	−0.24	0.50	−0.27	0.68	0.03	0.64	0.48	0.64	−0.19	0.84	0.08	0.25
Non-native forb	**−1.43****	**0.26**	**−1.85****	**0.38**	**0.36**	**<0.05**	**−3.85****	**0.67**	**−3.91****	**1.05**	**0.62**	**<0.05**
Root	**0.31**	**0.31**	**1.61****	**0.34**	**0.34**	**<0.05**	**15.65****	**0.31**	**17.65****	**0.31**	**0.47**	**<0.05**
Animal												
Deer & Bighorn	0.21	0.48	−0.74	0.61	0.11	0.05	**−0.45**	**0.40**	**−1.40****	**0.58**	**0.17**	**<0.05**
Elk	**2.00****	**0.70**	**−0.12**	**0.90**	**0.24**	**<0.05**	**2.04****	**0.61**	**1.47****	**0.69**	**0.20**	**<0.05**
Moose	15.66**	0.48	NA[c]	NA[c]	0.10	0.06	**17.26****	**0.57**	**14.50****	**1.14**	**0.32**	**<0.05**
Small mammal	1.09	0.66	0.67	0.74	0.10	0.07	15.48**	0.27	15.89**	0.46	0.10	0.14
Insect	−0.00	0.53	−0.28	0.62	0.03	0.56	−1.18	1.43	0.01	1.28	0.07	0.28

[a] coefficient estimated from GLM

[b] model fit assessed based on correlation between predicted values fitted via GLM and observed dependent variable values. Models with good fit ($\alpha = 0.05$) are in bold

[c] moose was not detected in scat samples collected in the mountains and on reclaimed mines

*significance at $\alpha = 0.05$ level; **significance at $\alpha = 0.10$ level

Table 4.4: Variation in grizzly bear food availability by land designation. Availability was assessed by sampling presence/absence of major bear foods in 20×20 m plots ($n_{foothills}$ = 494; $n_{mountains}$ = 225; $n_{reclaimed\ mines}$ = 166). Reclaimed mines were withheld as the reference category in all models run.

	Fth		**Mt**		**Wald**[b]			**Link test**[b]	
Food category	β_i[a]	Robust SE	β_i	Robust SE	χ^2	*df*	P_{Wald}	P_{hat}	P_{hatsq}
Plant									
Berry	__3.79**__	**0.28**	__1.56**__	**0.22**	188.35	2	<0.05	<0.05	1
Graminoid	0.81**	0.35	0.57	0.40	5.33	2	0.07	0.94	1
Native forb	__1.44**__	**0.20**	__0.69**__	**0.23**	62.49	2	<0.05	<0.05	1
Non-native forb	__−1.48**__	**0.19**	__−2.75**__	**0.27**	111.90	2	<0.05	<0.05	1
Root	__1.06**__	**0.37**	__2.15**__	**0.37**	51.11	2	<0.05	0.11	1
Animal									
Deer & Bighorn	__−1.20**__	**0.19**	__−0.72**__	**0.21**	41.39	2	<0.05	<0.05	1
Elk	__−0.59**__	**0.019**	__−0.44**__	**0.21**	10.04	2	<0.05	0.74	1
Moose	__1.46**__	**0.41**	__0.80*__	**0.45**	17.20	2	<0.05	0.70	1

[a] coefficient estimated from logistic regression

[b] models with good fit (α = 0.05) are in bold

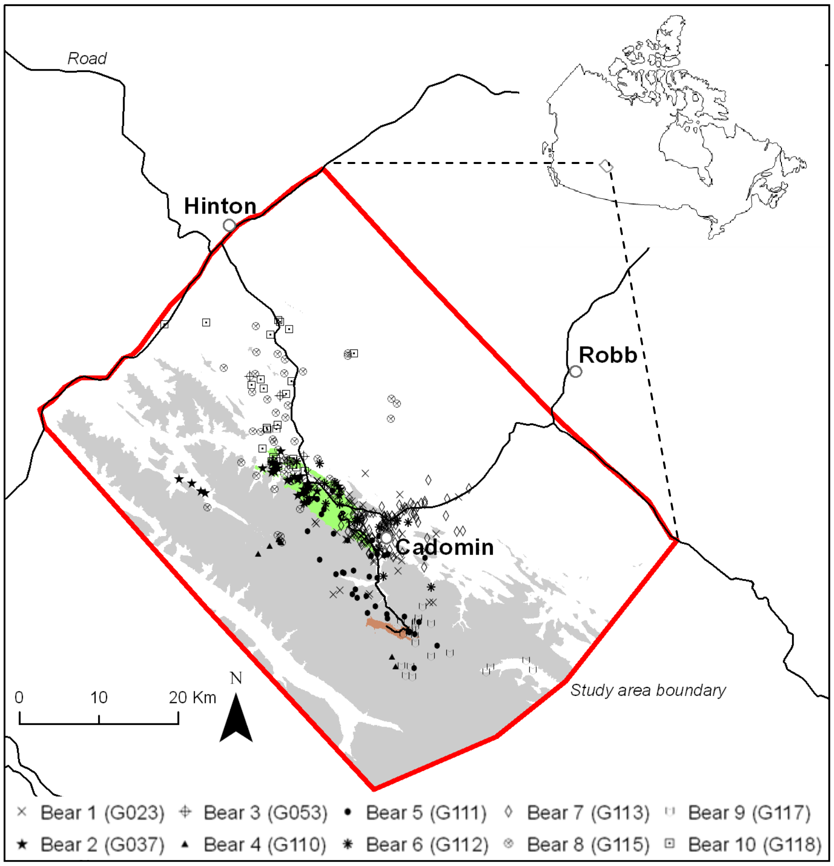

Figure 4.1: Study area for grizzly bear diet in west-central Alberta, Canada, including major roads, towns (empty dots) and colour coded mine disturbance areas: reclaimed mines (green), active mine (brown). Grizzly bear (by individual) GPS location clusters visited in 2009-2010 are overlaid on mountains (≥1,700 m; gray) and foothills (<1,700 m; white). Only clusters with evidence of feeding (*n* = 234) and/or where scat was collected (*n* = 331) are shown.

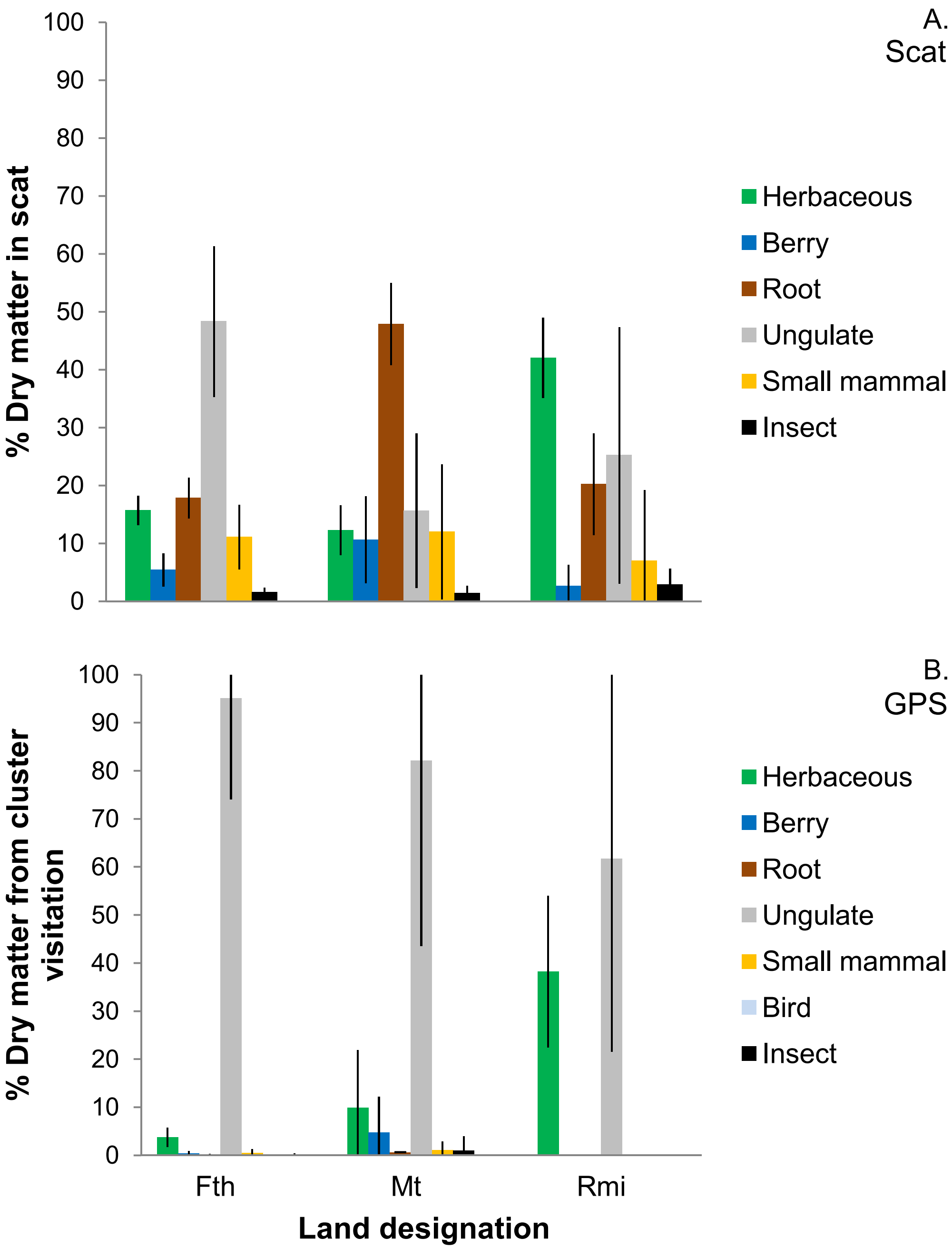

Figure 4.2: Diet of grizzly bears in west-central Alberta by land designation (Fth - foothills, Mt - mountains, Rmi - reclaimed mines), using two methods: scat analysis (A) and GPS location cluster visitation (B). Error bars are means ± 95% CI. Confidence intervals for the GPS cluster method are truncated at 100%.

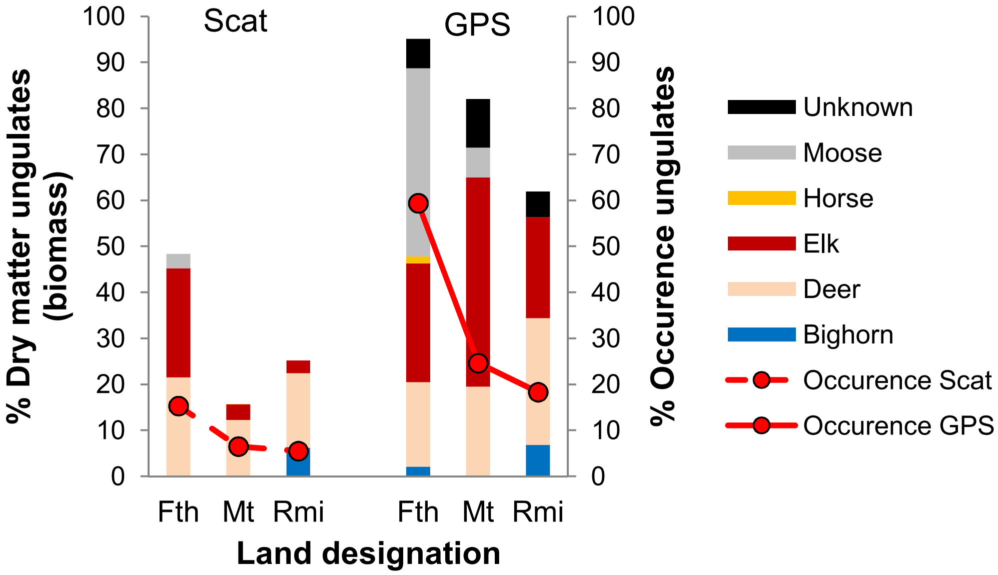

Figure 4.3: Ungulate consumption by grizzly bears in west-central Alberta by land designation (Fth - foothills, Mt - mountains, Rmi - reclaimed mines), using two methods: scat analysis and GPS location cluster visitation. The primary vertical axis represents % biomass whereas the secondary vertical axis is % occurrence of ungulates relative to total items in scat. Sample sizes (number of items/taxonomically identifiable subitems) were comparable for scat analysis ($n_{foothills}$ = 77/1276; $n_{mountains}$ = 13/208; $n_{reclaimed\ mine}$ = 9/133) and GPS field visitation ($n_{foothills}$ = 98/NA; $n_{mountains}$ = 16/NA; $n_{reclaimed\ mines}$ = 13/NA).

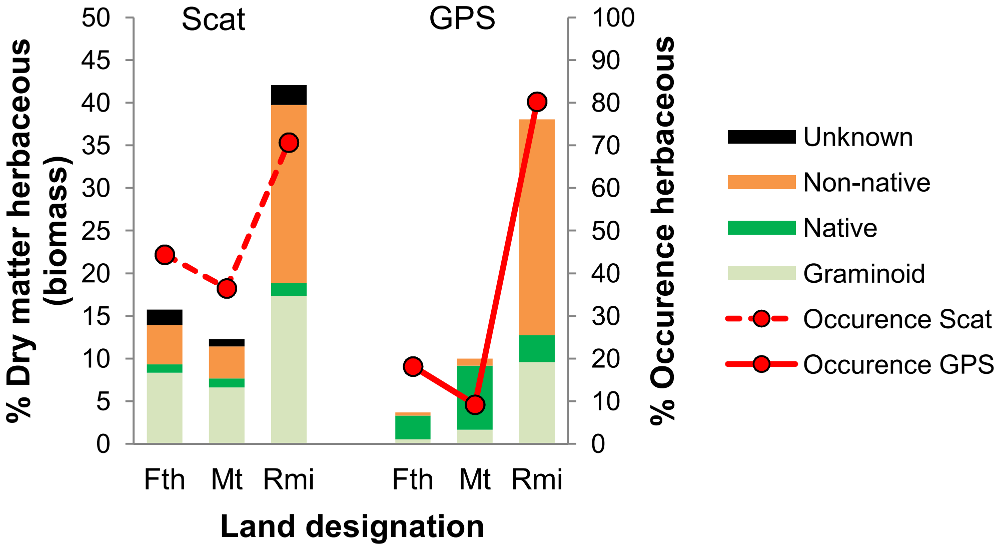

Figure 4.4: Herbaceous diet of grizzly bears in west-central Alberta by land designation (Fth - foothills, Mt - mountains, Rmi - reclaimed mines), using two methods: scat analysis and GPS location cluster visitation. The primary vertical axis represents % biomass whereas the secondary vertical axis is % occurrence of herbaceous food items relative to total items in scat. Sample sizes (number of items/taxonomically identifiable subitems) were much larger for scat analysis ($n_{foothills}$ = 223/1535; $n_{mountains}$ = 73/559; $n_{reclaimed\ mine}$ = 116/940) compared to GPS field visitation ($n_{foothills}$ = 30/NA; $n_{mountains}$ = 6/NA; $n_{reclaimed\ mines}$ = 57/NA).

SUPPLEMENTARY MATERIAL

Table S.1: Adjusted scat correction factors for ungulate biomass estimated to have been ingested by grizzly bears. Original correction factors from Hewitt were modified to reflect field evidence at GPS location kill clusters (*n* = 124) visited in west-central Alberta in 2009-2010.

Period	CF*	Assumption	Justification
Den emergence - May 14	1	90% hair ingestion	Scavenging (cougar and wolf kills)
May 15 - June 14	1.5	60% hair ingestion	Predation young neonate ungulates
June 15 - July 14	2	45% hair ingestion	Predation neonate ungulates
July 15 - September 14	1.5	60% hair ingestion	Predation and scavenging (cougar and wolf kills)
September 15 - Denning	1	90% hair ingestion	Scavenging (cougar, wolf and hunter kills)

* CF - correction factor. Further details are provided in the 'Methods' section under 'Biomass estimation'.

Table S.2: Listing of food items that occurred in grizzly bear diet in west-central Alberta during 2009-2010. Strikethrough represents herbaceous plant species that were considered *a priori* to occur in grizzly bear diet, for which reference collections were available, but which were not found through scat analysis or at GPS location clusters.

Broad group	**Plant**	**Foothills**	**Mountains**	**Reclaimed mines**
Root	*Hedysarum spp.*	++	++	+
Herbaceous (Native)	*Achillea milefolium*	+		
	~~*Aster spp.*~~			
	~~*Claytonia lanceolata*~~			
	Epilobium angustifolium	+		+
	Equisetum spp.	++	+	++
	~~*Galium boreale*~~			
	~~*Glycyrrhiza lepidota*~~			
	Heracleum lanatum	++	+	+
	Lathyrus ochroleucus	+		
	Pedicularis bracteosa	+		
	Senecio triangularis		+	
	~~*Thalictrum spp.*~~			
	Valeriana sitchensis			+
	~~*Vicia americana*~~			
Herbaceous (Non-native)	*Astragalus cicer*			+
	Medicago spp.	+	+	++
	Melilotus spp.	+	+	++
	Taraxacum officinale	+	+	+
	Trifolium spp.	++	+	++
Herbaceous (Native & Non-native)	Graminoids	++	++	++
	Unknown herbaceous	+	+	+
Berry	*Arctostaphylos spp.*	+	+	+
	Cornus canadensis	+		
	Empetrum nigrum	+	+	
	Fragaria spp.		+	
	Lonicera spp.	+		+
	Ribes spp.	+	+	
	Rosa spp.	++		
	Rubus idaea	+		+

Table S.2 Continued

Broad group	Plant	Foothills	Mountains	Reclaimed mines
	Shepherdia canadensis	+	++	+
	Vaccinium caespitosum	+	++	+
	V.membranaceum	+	+	
	V. myrtillus	+		+
	V. scoparium	+	+	
	V. uliginosum	+		
	V. vitis-idaea	+		
	Unknown berry	+		
Ungulate	*Alces alces*	++	+	
	Cervus elaphus	++	++	+
	Equus caballus	+	+	
	Odocoileus spp.	++	++	++
	Ovis canadensis	++		++
	Unknown *Ungulata*	+	+	+
Small mammal	*Castor canadensis*	+	+	
	Leporidae	++		+
	Mustelidae	+	++	
	Ondatra zibethicus	+		+
	Soricidae	+	+	+
	Sciurus/Tamiasciurus	++	++	+
	Spermophilus/Tamias/Urocitellus	+	+	+
	Unknown *Rodentia*	++	+	+
Bird	*Tetraonidae*	+	+	
Insect	*Coleoptera*	+		
	Formicidae	++	++	++

\+ occurred in bear diet based on either GPS cluster visitation or scat analysis

++ occurred in bear diet based on both methods

Table S.3: Total (Tot) and Relative (Rel) Biomass (B) of food items that occurred in grizzly bear diet in west-central Alberta during 2009-2010. Relative biomass was obtained by dividing total biomass for a specific food by the total biomass for the respective method and land designation (Fth - foothills, Mt - mountains, Rmi - reclaimed mines), and multiplying the result by 100.

			Scat						**GPS**					
		CF*	Fth		Mt		Rmi		Fth		Mt		Rmi	
Food category	Taxonomy		Tot B	Rel B	Tot B	Rel B	Tot B	Rel B	Tot B	Rel B	Tot B	Rel B	Tot B	Rel B
Plant														
Herbac. (Native)	*Achillea millefolium*	0.3	0	0	0	0	0	0	0.2	0.1	0	0	0	0
	Epilobium angustifolium	0.3	0	0	0	0	0	0	0.8	0.3	0	0	0.5	1.0
	Equisetum spp.	0.2	99.8	0.9	42.8	1.0	35.8	1.5	1.1	0.3	0	0	0.2	0.3
	Heracleum lanatum	0.3	3.6	0	0	0	0	0	6.7	2.1	1.8	5.0	0.3	0.5
	Lathyrus ochroleucus	0.3	3.8	0	0	0	0	0	0	0	0	0	0	0
	Pedicularis bracteosa	0.3	0	0	0	0	0	0	0.1	0	0	0	0	0
	Senecio triangularis	0.3	0	0	0	0	0	0	0	0	0.9	2.5	0	0
	Valeriana spp.	0.3	0	0	0	0	0	0	0	0	0	0	0.2	0.3
Herbac. (Non-Native)	*Astragalus cicer*	0.3	0	0	0	0	0	0	0	0	0	0	3.1	6.2
	Medicago spp.	0.3	50.4	0.5	18.6	0.5	11.1	0.5	0	0	0	0	5.6	11.4
	Melilotus spp.	0.3	23.2	0.2	1.7	0	15.9	0.7	0	0	0	0	0.3	0.5
	Taraxacum officinale	0.3	0	0	0	0	0	0	0.2	0.1	0.3	0.8	0.5	1.0
	Trifolium spp.	0.3	435.1	4.0	134.6	3.3	470.3	19.7	1.1	0.3	0	0	3.5	7.2
Herbac. (Native & Non-native)	Graminoids	0.2	915.3	8.3	272.0	6.6	413.8	17.4	1.8	0.5	0.6	1.7	4.7	9.6
	Unknown herbaceous	0.3	195.6	1.8	36.1	0.9	54.7	2.3	0	0	0	0	0	0
Berry	*Arctostaphylos spp.*	0.9	7.4	0.1	4.2	0.1	21.2	0.9	0	0	0	0	0	0
	Cornus canadensis	0.9	2.8	0	0	0	0	0	0	0	0	0	0	0
	Empetrum nigrum	0.9	111.3	1.0	251.7	6.1	0	0	0	0	0	0	0	0
	Fragaria spp.	0.9	0	0	1.9	0	0	0	0	0	0	0	0	0
	Lonicera spp.	0.9	8.4	0.1	0	0	5.6	0.2	0	0	0	0	0	0
	Ribes spp.	0.9	0	0	7.4	0.2	0	0	0.1	0	0	0	0	0
	Rosa spp.	0.9	0.2	0	0	0	0	0	0.9	0.3	0	0	0	0
	Rubus idaea	0.9	22.3	0.2	0	0	13.0	0.5	0	0	0	0	0	0
	Shepherdia canadensis	1.8	108.3	1.0	14.7	0.4	20.6	0.9	0	0	0.2	0.7	0	0
	Vaccinium caespitosum	0.5	112.9	1.0	0.9	0	2.2	0.1	0	0	1.3	3.6	0	0
	V.membranaceum	0.5	0	0	0	0	0	0	0.2	0.1	0.2	0.5	0	0
	V. myrtillus	0.5	4.3	0	0	0	0.5	0	0	0	0	0	0	0
	V. scoparium	0.5	167.0	1.5	157.7	3.8	0	0	0	0	0	0	0	0

Table S.3 Continued

			Scat						GPS					
		CF*	Fth		Mt		Rmi		Fth		Mt		Rmi	
Food category	Taxonomy		Tot B	Rel B	Tot B	Rel B	Tot B	Rel B	Tot B	Rel B	Tot B	Rel B	Tot B	Rel B
	V. uliginosum	0.5	1.6	0	0	0	0	0	0	0	0	0	0	0
	V. vitis-idaea	0.5	1.6	0	0	0	0	0	0	0	0	0	0	0
	Unknown berry	0.9	48.4	0.4	0	0	0	0	0	0	0	0	0	0
Root	*Hedysarum* spp.	1.0	1960.7	17.9	1971.9	47.9	482.0	20.2	0.2	0.1	0.2	0.7	0	0
Animal														
Ungulate	*Alces alces*	Varied+	344.5	3.1	0	0	0	0	133.2	40.9	2.3	6.5	0	0
	Cervus elaphus	Varied+	2600.4	23.7	140.0	3.4	67.3	2.8	84.0	25.8	16.4	45.5	10.8	22.0
	Equus caballus	Varied+	0	0	0.4	0	0	0	4.8	1.5	0	0	0	0
	Odocoileus spp.	Varied+	2356.8	21.5	504.0	12.2	385.5	16.2	59.8	18.4	7.0	19.5	13.6	27.5
	Ovis Canadensis	Varied+	4.0	0.0	0	0	148.5	6.2	6.9	2.1	0	0	3.4	6.8
	Unknown *Ungulata*	Varied+	0	0	0	0	0	0	21.0	6.4	3.8	10.5	2.8	5.6
Small mammal	*Castor canadensis*	1.5	46.9	0.4	7.4	0.2	0	0	0	0	0	0	0	0
	Leporidae	1.5	31.6	0.3	0	0	7.5	0.3	1.7	0.5	0	0	0	0
	Mustelidae	1.5	30.5	0.3	127.4	3.1	0	0	0	0	0.3	0.9	0	0
	Ondatra zibethicus	1.5	9.0	0.1	0	0	5.3	0.2	0	0	0	0	0	0
	Soricidae	1.5	93.8	0.9	40.3	1.0	6.0	0.3	0	0	0	0	0	0
	Sciurus/Tamiasciurus	1.5	674.9	6.1	234.4	5.7	0.4	0	0.1	0	0.1	0.2	0	0
	Spermophilus/Tamias/ Urocitellus	1.5	226.1	2.1	86.6	2.1	145.5	6.1	0	0	0	0	0	0
	Unknown *Rodentia*	1.5	104.2	0.9	0	0	1.5	0.1	0	0	0	0	0	0
Bird	*Tetraonidae*	NA	0	0	0	0	0	0	0.5	0.2	0.5	1.4	0	0
Insect	*Coleoptera*	1.1	5.5	0.1	0	0	0	0	0	0	0	0	0	0
	Formicidae	1.1	165.1	1.5	60.4	1.5	68.2	2.9	0	0	0	0	0	0
Total (dry matter)		NA	10977.0	100	4117.0	100	2382.2	100	325.5	100	35.9	100	49.4	100

* CF - correction factor. Further details are provided in the 'Methods' section under 'Biomass estimation'.

+ Correction factors incorporated knowledge of bear consumption of ungulates according to season, taking into consideration ungulate body size and predation versus scavenging events, based on GPS location cluster visitation (Table S.1)

CHAPTER 5

GRIZZLY BEAR UNGULATE CONSUMPTION SITES AND THE RELEVANCE OF PREY SIZE TO BEHAVIOUR AT KILL SITES

ABSTRACT

Consumption of prey forms a large part of prey handling time and knowledge of where prey is eaten can inform management of predator-prey systems. Safeguarding habitat features that promote prey consumption can be important for enhancing large populations of facultative or obligate carnivores of conservation concern. I investigated habitat characteristics at 124 sites where radiocollared adult grizzly bears (*Ursus arctos*) (n = 9) consumed ungulates and contrasted these with paired random sites. I ranked *a priori* hypotheses incorporating the potential effects of prey distribution, human and scavenger-derived risks on the selection of consumption sites. To further partition energetic trade-offs in prey consumption, I characterized behaviours at kill sites and evaluated multiple hypotheses on factors determining grizzly bear food caching. Ungulates were consumed in forested areas, close to habitat edges, and where horizontal cover was high; the latter possibly suggesting a mechanism to avoid carcass detection by scavengers. Distance to roads had no effect on prey consumption sites but ungulate carcasses were further from trails than expected suggesting another strategy to deter kleptoparasitism. Models incorporating presence/absence of key non-ungulate bear foods had little weight of evidence, suggesting that intra-specific competition might not be an important factor in the selection of ungulate consumption sites in this low-density grizzly bear population if most bears hunt or scavenge opportunistically. I found no support for the resource pulse and food-spoilage caching hypotheses and demonstrated that prey size is the main driver of grizzly bear caching behaviour. Although bears chose sites that minimized risk of losing prey to scavengers and they were more likely to cache large prey, caching was not always effective and large ungulates were more

likely to be detected by scavengers. Once scavengers arrived at the site, bears defended the carcasses.

INTRODUCTION

Habitat loss affects biodiversity and threatens the persistence of many top predator species (Weber and Rabinowitz 1996, Gittleman et al. 2001, Caro and Sherman 2011). Conservation decisions benefit from data on habitat requirements (Davidson et al. 2009) in relation to fitness (Mitchell and Hebblewhite 2012), and behaviour of top predators interacting with prey and competitors (Ritchie and Johnson 2009, Finke and Snyder 2010). Such data are particularly relevant in the context of landscape conversion, which can trigger shifts in species ranges (Laliberte and Ripple 2004). This knowledge also might help to mitigate human-predator conflict which is often a problem at the periphery of protected areas (Woodroffe and Ginsberg 1998) and wherever human encroachment occurs in predator range (Treves and Karanth 2003).

For many wide-ranging, free-roaming mammalian predators in forested environments where direct observations are difficult, little information exists on the duration of prey consumption and habitat features at sites where meat is consumed. Prey consumption time (kill handling time/time spent at kill) is an essential component of predator-prey relationships, in addition to time to search, capture and kill (time to kill) (Holling 1959). The concept of consumption time also could be applied if prey were scavenged, although it is not the same as kill handling time which refers to predation. Consumption time is readily obtained using GPS radiotechnologies (Merrill et al. 2010) and studies that employ these technologies can decrease the bias associated with documenting prey consumption time by direct observations in open environments or during daytime only (Webb et al. 2008, Knopff et al. 2009).

If prey consumption is lengthy it could lead to high risk human-predator encounters at consumption sites. Such conflicts are more likely for carnivores that defend carcasses such as African lions (*Panthera leo*) (Kissui 2008) or grizzly bears (*Ursus arctos*) (Quigley and Herrero 2005), although carnivores can adjust behaviourally to reduce risk of encounters with people (Valeix et al. 2012). Longer consumption times for solitary carnivores such as cougars (*Puma concolor*) (Knopff et al. 2009) may set these more at risk of conflict at the consumption site than group-living predators that have shorter consumption times (Webb et al. 2008).

Habitat heterogeneity can influence each stage of predation, including consumption time (Gorini et al. 2011). In human-use areas carnivores and other animals may experience energetic loss (Ashenafi et al. 2005, Kolowski and Holekamp 2009) such as through fleeing, increased vigilance and decrease in effective habitat quality (Frid and Dill 2002). Knowledge of the sites where prey are consumed can be important if the management goal is to protect habitats that facilitate predator energetic gain (Koppel et al. 2005). In addition, identifying prey consumption habitats can facilitate strategies to mitigate human-carnivore conflict (Winterbach et al. 2012) and inform habitat manipulation to reduce predation in declining prey populations (Sinclair et al. 1998).

Because of wide-ranging movements, seasonal habitat requirements, low reproductive rates, and risk of conflict with people (Weaver et al. 1996, Mattson and Merrill 2002), the grizzly bear has declined throughout much of its range. Habitats have become fragmented (Proctor et al. 2012) and the current range of the species is a 53% contraction compared to the historical range (Laliberte and Ripple 2004). The grizzly bear in Alberta, Canada was designated as Threatened by the provincial government in 2010. In west-central Alberta, grizzlies persist at low densities in the interface between largely pristine mountainous areas and heavily developed Foothills. Similar to other interior populations of grizzly bears (Jacoby et al. 1999, Mowat and Heard 2006, Zager and Beecham 2006), ungulates form an important part of the diet of Alberta bears particularly in late spring and early summer during ungulate calving and fawning season (Munro et al. 2006). At this time of the year the ungulate population peaks, and ungulates in their first weeks of life can be outrun by predatory bears (Craighead 2000). Ungulates are part of a bear's diet during the remainder of the active season (outside denning) as well, primarily by scavenging other predator kills or in the form of winter-killed carrion (Mattson 1997, Wilmers et al. 2003a).

The motivation behind meat consumption by bears stems from its high nutritional value, as animal food items have more protein than vegetative items, and the carnivorous gastro-intestinal tract (Schwab et al. 2009) enables more effective digestion of animal than plant matter (Pritchard and Robbins 1990). Meat in the diet of grizzly bears is correlated with body mass (Hilderbrand et al. 1999a, Hilderbrand et al. 1999b) possibly influencing fitness if larger bears have greater fitness than smaller ones (Mowat and Heard 2006).

Although meat is highly sought after with clear benefits to bears, if meat consumption occurs in human use areas, it can lead to undesired human-bear encounters (Northrup et al. 2012). Such conflicts can be exacerbated by the expansion of ungulate populations associated with human-induced habitat change (Latham et al. 2011b), if bears key in on this expanding food source. Knowledge of where bears consume ungulates can be used proactively to prevent human-bear dangerous encounters. Few data exist on grizzly bear habitat choice and consumption times of ungulates in forested environments.

Even though expanding populations of ungulates might bring more meat consumption opportunities to top predators, the habitat change that triggered ungulate range expansion also contributes to mesocarnivore range shifts in North America, with the coyote (*Canis latrans*) experiencing a 40% range expansion (Prugh et al. 2009). Coyotes scavenge on ungulate kills made by cougars (Ruth et al. 2010) and wolves (*Canis lupus*) (Wilmers et al. 2003b), but no study has yet documented coyote scavenging on grizzly bear kills. To minimize kleptoparasitism such as by coyotes or avian scavengers, which also can be substantial (Stahler et al. 2002), top predators may evoke evolutionary strategies such as caching prey, defending the kill, or a combination of the two. Caching as a form of food storage is a strategy to avoid food shortage (Smith and Reichman 1984). Caching has been documented in birds (e.g., shrike [*Lanius* spp.])

(Hernandez 1995) as well as many mammals, for example cougar (Laundre and Hernandez 2003), wolverine (*Gulo gulo*) (Wright and Ernst 2004), badger (*Taxidea taxus*) (Michener 2000), Arctic fox (*Vulpes lagopus*) (Careau et al. 2007, Careau et al. 2008), Eurasian lynx (*Lynx lynx*) (Podgorski et al. 2008), marten (*Martes americana*) (Henry et al. 1990), and otter (*Lutra lutra*) (Lanszki et al. 2006).

In theory, prey caching should preserve food for later use while minimizing detection by other scavengers, but few studies have documented large predator caching behaviour and caching success because of safety concerns and the difficulty of locating caches in complex environments. If scavengers effectively detect and consume prey killed by top predators, the predator that made the kill suffers a net energetic loss from the combined costs of locating, chasing, killing, caching prey and subsequent travel to return to the cache site. Alternatively, if the predator defends subdued prey, energetic losses might still be high if confronting group-living scavengers. Coyotes often travel in packs and up to 5 individuals have been recorded routinely at wolf-killed carcasses in the Yellowstone range (Wilmers et al. 2003b). If in large numbers, coyotes occasionally chase wolves away from carcasses (Merkle et al. 2009) and can displace cougars from kills (Harrison 1990). Kleptoparasitism thus can decrease fitness of the victim (Reader 2003) and kleptoparasitism rates vary with habitat change that shifts the proportion of predator to kleptoparasite (Honer et al. 2002). Investigating loss of prey by low-density populations of large obligate or facultative carnivores affected by habitat conversion to the benefit of expanding mesocarnivores, can assist large carnivore conservation.

In this study I identify habitat features associated with ungulate predation by bears and I investigate kill-site behaviour, including factors that determine the success of caching. The related European brown bears are known to cache meat by digging the ground and dragging litter, moss and debris on top of prey (Elgmork 1982), but records of caching behaviour for both North American grizzly bears and European brown bears have been opportunistic and sparse.

Elgmork (1982) identified sixteen caching sites by brown bears in Scandinavia, and Barker and Derocher (2009) observed two caches of broad whitefish (*Coregonus nasus*) made by barren ground grizzly bears. One hypothesis is that caching behaviour occurs for resources that take long to consume (Careau et al. 2007). An alternative hypothesis is that caching is a strategy employed to secure food during resource pulses (Careau et al. 2008) or during harsh environmental conditions associated with food shortage (Lanszki et al. 2006). On the other hand, caching might occur to avoid food spoilage which is more likely when ambient temperatures and humidity are high, such as at low elevations and on moist sites (Bischoff-Mattson and Mattson 2009).

Our goal is two-fold: 1. identify habitats conducive of ungulate consumption, thus informing habitat conservation or human-bear conflict prevention, and 2. evaluate competing hypotheses for explaining the motivation behind caching behaviour. I predict that to minimize detectability by scavengers grizzly bears preferentially consume ungulates in areas with low probability of presence of ungulates and other bears foods, away from roads, trails and habitat edges, and where horizontal cover is high. I hypothesize (1) that caching is more likely for larger prey requiring higher consumption time (prey size hypothesis), or (2) during the seasonal resource pulse of ungulate calving (resource pulse hypothesis). I also hypothesize that bears (3) are more likely to cache at lower elevations, under low vertical cover and on wet sites to avoid spoilage of meat (resource spoilage hypothesis). I predict that cached ungulates are less likely to be kleptoparasitised and bears would spend more time defending large ungulate carcasses.

METHODS

Study Area

The 3,200 km^2 study area was located in west-central Alberta, Canada at the interface between the eastern slopes of the Rocky Mountains and foothills (Figure 5.1). Elevation and ruggedness are greater in the western section which is mountainous with the eastern section being characterised by rolling hills. The predominant natural land cover is coniferous forest composed of white (*Picea glauca*), black (*P. mariana*) and Engelmann spruce (*P. engelmannii*), lodgepole pine (*Pinus contorta*), balsam (*Abies balasamea*) and subalpine fir (*A. lasiocarpa*). Mixed and deciduous forests also occur in the study area primarily at lower elevations and on sunny south facing slopes and include trembling aspen (*Populus tremuloides*) and balsam polar (*P. balsamifera*).

Grizzly bear foods in the study area are diverse (Nielsen et al. 2010), with the primary foods being sweetvetch roots (*Hedysarum* spp.), a variety of herbaceous plants and berries as well as ungulates including elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed (*Odocoileus virginianus*) and mule deer (*O. hemionus*), and bighorn sheep (*Ovis canadensis*) (Munro et al. 2006). Grizzly bears coexist with wolves, cougars and American black bears (*Ursus americanus*), as well as mesocarnivores such as coyotes, Canada lynx (*Lynx canadensis*), and red fox (*Vulpes vulpes*).

The eastern side of the study area is primarily Crown land with human activities including open-pit coal mining, forest harvesting, oil and gas development and extensive recreation (All Terrain Vehicles, hunting, horseback riding, mountain biking, hiking and camping). The western side is primarily protected provincially (Whitehorse Wildland Park) and federally (Jasper National Park), with a small amount of Crown lands, two reclaimed coal mines, one operational mine and a cement quarry with employees commuting daily. Only one permanent human settlement (Cadomin) with a population of 60 is present in the study area. The area is bordered to the north by a major highway and the Crown lands have a complex network of roads and trails used by oil and gas companies, forestry and recreation.

Data Collection

In spring/early summer and fall 2008−2010 I captured and deployed remotely downloadable GPS radiocollars (Telus UHF; Followit, Lindesberg, Sweden) on adult grizzly bears. With assistance from the Foothills Research Institute Grizzly Bear Program (Hinton, Alberta) I used baited culvert traps, aerial darting from a helicopter and limited leg-hold snaring (Cattet et al. 2008) and attempted to capture bears on reclaimed mines, protected areas (Whitehorse Wildland Park) and Crown lands to reduce bias in sampling bears that might have used only one land designation. All bears were captured and handled according to University of Alberta and University of Saskatchewan protocols for Animal Care and Use.

I programmed radiocollars to acquire a location every hour, 24 h/day, during March 15 to December 1 when the bears were mostly outside their winter dens. Every month of the monitoring period I radio located individual bears from the ground, fixed-wing aircraft or helicopter. To acquire GPS locations remotely from the radiocollars, once a month I approached each bear to within a safe distance that minimized disturbance to the animal, triangulating its position if on foot (>200 m). To identify clusters from monthly GPS datasets, I used a cluster algorithm developed by Knopff et al. (2009) which I modified for 1-h location inputs and 50 m distance between the two initial points in a cluster. I set a cut-off of minimum 3 hours for cluster duration, selected the 4 clusters with the largest number of locations from each bear each month (May-November) and randomly other clusters for field visitation. I uploaded cluster geometric centroids to hand-held GPS to access cluster locations by truck, ATV, helicopter, and on foot. I visited clusters 41 ± 15 days after the first fix in the cluster because of safety concerns (bears defending or returning to carcasses), caution to avoid disturbing the animals, and logistical limitations. This is comparable with the field visitation within 45 days of cluster occurrence in the Webb et al. (2008) wolf study and lower than 201 days from cluster occurrence in the Anderson and Lindzey (2003) cougar study.

Upon arrival at the cluster centroid, even though most often the ungulate consumption site was obvious, crews undertook a thorough search of the area on a radius of 50 m from the centroid to search for additional carcass remains and sign of other predators with reference to the cluster date(s). I recorded whether a cache was present and centred a 20×20-m habitat survey plot on the cache or, for sites with no cache, I centred the plot on the location where most carcass remains were found, typically with a bear bed in the immediate vicinity. The Wide Area Augmentation System (WAAS) enabled Garmin units most often brought me within ~5 m from the consumption location. I was typically unable to assess the exact location of where the actual kill had been made but I could locate the site where the bear had consumed the ungulate based on cache evidence, presence of bear bed(s) and scat near the remains.

I assigned species, age and sex to each carcass and estimated case-specific ungulate biomass (prey size) following the methods of Knopff et al. (2010a). Bear behaviour at the site was classified as either predation, scavenging or unknown, with ungulate cause of death assigned based on whether the age of the remains closely matched the dates during which the cluster was created (Knopff et al. 2010b), bear predation sign (punctured skull, fractured large ungulate spine), and evidence of other predator presence (scat, hair mat and sheared-hair characteristic of cougar predation, cracked long bones and widely scattered bones characteristic of canid use of carcass). Close investigation of bear and scavenger scat to determine relative freshness based on moisture, odour strength, presence/absence of mold, colour (Wasser et al. 2004) and aspect (original shape preserved/shape lost) and assessment in relation to cluster date validated the ungulate cause of death and provided data on kleptoparasitism of carcasses. In assigning scat age I attempted to take into account site exposure to the sun, elevation at the site and local weather patterns (i.e., precipitation) during previous weeks.

I replicated the search for a carcass and the habitat-sampling protocol described below at one location 300 m away on one of four cardinal directions from the consumption site, with subsequent directions being chosen clockwise (N, E, S and W respectively). I chose 300 m based on movement rates of adult bears (annual mean step length 269 m/h outside winter denning, range 175−367 based on 11 adult bears monitored in the area before this study). I classified each site (habitat survey plot) as barren land (<5% vegetated), herbaceous (>5% vegetated, <5% shrub cover, <5% tree cc), shrub (>5% shrub cover, <5% tree cc), mixed forest (21-79% conifer), open conifer (5-30% cc, >80% conifer), moderate conifer (31-69% cc, >80% conifer), or dense conifer (>70% cc, >80% conifer). I considered horizontal cover, stand basal area and distance to nearest trail as variables that might influence visual and potential olfactory detectability of a carcass by other predators. I adapted the method described by Nudds (1977) to assess horizontal cover (visibility) at the consumption site using a foldable sheet with alternating red and white rectangles (50×30.48-cm). One technician stood at the carcass location holding the sheet vertically and the second technician took two horizontal cover readings from 10 m away on a north and south direction respectively. Readings were taken at 0.5 and 1 m from the ground to account for the low height of a carcass, and averaged for analyses. For treed plots, I used a 2-m factor prism to estimate stand basal area for live and dead trees separately and also estimated forest age as immature, mature or old based on tree diameter and elevation. Using a combination of field observations, 2-m resolution colour ortho-imagery and knowledge of the area, I measured in ArcMap v.9.2 (ESRI, Redlands, California) the Euclidean distance from the consumption site (centre of the plot) to the nearest ATV/hiking trail/cutline (hereafter, trail), stream and habitat edge. Distance to nearest road was measured also, which along with distance to nearest trail accounted for the potential effect of human presence.

In addition, I recorded presence/absence of ungulate species based on pellet groups within the 20×20-m plot that appeared fresh. Elk, moose and deer contribute substantially (each >28% frequency of consumption) to the meat diet of bears monitored during this study (Chapter 4). I pooled data for deer and bighorn sheep because the pellets of these species cannot be reliably separated (Marshal et al. 2006). I accounted for differential detectability of ungulate pellets by recording snow cover in four percentage classes. Only sites at which snow cover was <25% were included in statistical analyses.

To account for possible consumption site choice to avoid other bears, I recorded percentages cover for nine forb and legume species known to be important for grizzly bear grazing in the region (Nielsen et al. 2003, Munro et al. 2006), by using five 0.7×0.7-m quadrants distributed at 5 m intervals along a 20 m N−S transect through the centre of each plot. Because of concerns with differential growth rates of plants in the elapsed time between cluster formation and field visitation, I derived presence-absence data from the percentage cover data. Monocots were excluded from statistical analyses because they occurred at nearly all sites (96%). Also, the presence/absence of eleven berry shrubs used by grizzly bears in the area (Nielsen et al. 2003, Nielsen et al. 2010) was recorded in the quadrants. When snow was present at the sites during field visitation, I still recorded ground vegetation after clearing the snow from quadrants.

I considered vertical cover, elevation, solar insulation and moisture as potential variables that influence carcass spoilage. I used a spherical densiometer (Lemmon 1956) to record percentage vertical cover for the site, averaging 4 readings (one in each cardinal direction) at each of the 5 quadrant locations on the north-south transect. Elevation (m) was recorded from a barometric altimeter on the GPS unit. I accounted for solar insulation and moisture by deriving the Nielsen and Haney (1998) site severity index (SSI) modified from the Beer's aspect transformation (Beers et al. 1966). The index incorporates slope and aspect, northeast slopes having the lowest solar insulation and highest moisture (low index values) and southwest slopes having the highest solar insulation and xeric moisture (high index values).

Modeling Habitat where Grizzly Bears Consume Ungulates

I used discrete-choice models (Cooper and Millspaugh 1999) based on conditional logistic regression to assess the factors (covariates) that influenced bear choice of sites for ungulate consumption. I used the entire dataset to model habitat choice because of sample size limitations that precluded separate analyses for predation, scavenging and unknown meat acquisition by bears. The matched design with one random site associated with each ungulate consumption site was a trade-off between sampling availability and maximizing field visitation of clusters that were potential ungulate consumption sites. In conditional logistic regression, the contrast in the binary response variable is constrained on the 1 values, in this instance the available location (0) being conditioned to spatially occur 300 m away from the location selected for site consumption (1). My data fit an used-unused sampling design with 0% contamination (*sensu* Keating and Cherry [2004]), as I found no evidence of consumption of ungulates at any of the paired random locations.

I created *a priori* models for ungulate consumption site choice based on ecological relevance of various factors that might influence where consumption sites occur. Habitat models tested multiple hypotheses which considered ungulate occurrence, risk of inter- and intra- specific kleptoparasitism as well as human risk as driving factors of site choice. I excluded variables that were highly correlated (Pearson correlation $|r|>0.6$) from the same model, estimated models with each of the correlated variables one at a time and kept the variable that best improved fit. I examined potential collinearity between linear predictor variables by using variance inflation factors (VIF) diagnostics. Variables that had individual VIF scores >10 or the mean of all VIF scores considerably larger than 1 were classified as collinear and not used in the same model structure (Chatterjee and Hadi 2006). These rules resulted in dropping stand basal area and forest age as they were highly correlated with each other and with vertical cover. I also excluded the habitat classification according to the 7 classes assigned during field visitation because of high correlations with vertical cover and ran a separate conditional logistic regression model to estimate selection coefficients for different habitat classes using a categorical variable for habitat as the predictor variable. Pooled barren land and herbaceous class was chosen as the reference category in contrasting habitat classes.

I tested the effects of quadratic terms on model performance and included squared terms for distance to nearest road, nearest trail, nearest edge and nearest stream to account for non-linearities in the predictor variables. I used robust clustering estimation of standard errors to account for unequal sample sizes (ungulate consumption sites) between different bears (Nielsen et al. 2002). This technique calculates the variance using the Huber-White sandwich estimator (Huber 1967, White 1982) allowing independence between bears (clusters) but not necessarily within clusters, resulting in parameters estimates and significance levels unbiased by individual variation.

For each land designation, I used ΔAICc (based on Akaike's Information Criterion corrected for small sample size) and Akaike weights to select the best models (Burnham and Anderson 1998, Anderson et al. 2000) from the set of candidate models. I evaluated model accuracy using the Receiver Operating Characteristic (ROC) Area Under the Curve (AUC) recommended by Boyce et al. (2002) for used-unused designs, where values of 0.9 and higher represented high model accuracy, 0.7−0.9 good model accuracy and values of 0.5−0.7 low model accuracy respectively (Swets 1988, Manel et al. 2001). I used the absolute minimum of the difference between sensitivity and specificity values to estimate the optimal probability cut-off for classifying presence-absence of ungulate consumption sites (Liu et al. 2005).

Caching and the Influence of Kleptoparasites on Behaviour at Kill Sites

I used logistic regression to test hypotheses on factors that could influence whether caching behaviour occurs (caching = 1; no caching = 0). I restricted the analyses to my grizzly bear predation data only (*n* = 63) to avoid confounding effects of not knowing the ungulate biomass available to the bear for scavenging and unknown meat acquisition events. Caching behaviour hypotheses I tested included the resource-pulse hypothesis, prey-size hypothesis, meat-spoilage hypothesis, and combinations thereof. I screened variables for correlations, assessed collinearity and used robust clustering to control for heteroskedasticity. I ranked candidate models using ΔAICc and Akaike weights, used ROC to evaluate model accuracy and estimated optimal probability cut-off to classify presence-absence of caching.

I was unable to test another classical hypothesis (kleptoparasitism risk) directly because I did not have an estimate of the distribution of other predators/scavengers in the region before a bear predation event. However, because I did have data on kleptoparasites that were present in the area after the kill was made, I was able to assess their influence on bear behaviour at kill sites.

I assessed whether cached ungulates were most likely to be detected by scavengers using logistic regression with scavenger scat presence as dependent variable (scavenger = 1; no scavenger = 0) and a categorical variable for cache presence/absence as predictor. I also assessed whether large prey were more likely to be detected using scavenger presence as dependent variable. Finally, for caching sites only, I assessed whether scavengers were present at the site regardless of how much time bears spent at the carcass.

RESULTS

I captured and deployed GPS radiocollars on 12 adult grizzly bears. Two males slipped their collars within a month of capture and nine of the ten remaining bears consumed ungulates during the monitoring period. The tenth bear was only monitored for 2.5 months during which he did not consume ungulates, but this bear did consume ungulates during a 2008 pilot study. The nine bears that were included in statistical analyses included females (n = 6) and males (n = 3) that were monitored for 383 bear-days during hypophagia (mean 7.1 bears), 629 bear-days in early hyperphagia (mean 11.6 bears) and 618 bear-days in late hyperphagia (mean 7.5 bears), with seasonal delineation following Nielsen et al. (2004a). The sample size (n = 9 adult bears) represents a substantial proportion of the grizzly bear population in the 3,200 km^2 study area, which has a population density of 4.79 bears/1,000 km^2 (Boulanger et al. 2005).

Grizzly Bear Consumption of Ungulates

During May-November 2009 and 2010 I located a total of 128 sites where radiocollared bears had consumed animal matter. Four sites at which bears had consumed birds (2x), one hare and one mustelid were excluded from analyses because of insufficient sample size for small-prey kill sites and because my focus was on sites where bears had consumed ungulates (*n* = 124). Of the 124 ungulate consumption sites which represented my sample size pooled across years and seasons (mean ± SE, 14 ± 4 sites, *range* 2−43), 50.8% of the sites were depredation sites, 35.5% were sites where bears had scavenged and 13.7% were classified as unknown. The majority of sites including all unknown consumption sites had one ungulate carcass, but 1.6% of depredation sites and 6.9% of scavenging sites had two carcasses, the latter representing cougar-killed prey. When two carcasses were present prey biomass calculation included the summed biomasses for both carcasses. Of 38 recorded grizzly bear scavenging events, most scavenging occurred on cougar kills (50%) followed by wolf kills (29%) and human-hunter-killed ungulates (21%).

Grizzly bears spent more time at larger ungulate carcasses that they had killed than at smaller ones ($r = 0.534$, $df = 61$, $P < 0.05$) (Figure 5.2), but this pattern was not apparent for scavenging sites ($r = 0.214$, $df = 37$, $P = 0.191$). Consumption time at ungulate carcasses was 19.4 ± 16.4 h at depredation sites (*range* = 3−94 h) and 33.2 ± 28.9 h at scavenging sites (*range* = 3−125 h).

Ungulate Consumption Habitat

The majority of sites were located on Crown lands (84.7%) and the small proportion of sites on reclaimed mines (10.5%), in protected areas (3.2%) and on active mine leases (1.6%) precluded analyses by land designation. As shown by the goodness-of-fit Wald chi-square test results (Table 5.1), the model for habitat class was significant, with consumption of ungulates more likely to occur in moderate and dense coniferous forests (Figure 5.3) but the model had low predictive power (AUC = 0.65). This overall pattern held for mined landscapes, with 11 out of 13 ungulate consumption sites on reclaimed mines in moderate and dense coniferous forest, and the 2 carcasses on an active mining lease also in dense coniferous forest.

Of the 12 candidate models tested, two of the top three included ungulates as well as detection by scavengers, and the third was an ungulate-only model (Table 5.2). The top model received substantial support ($\Delta_i < 2$), the second model received some support ($2 \leq \Delta_i < 4$), whereas the ungulate-only model received less support. All other models including those for detection by humans or other bears received very little ($7 \leq \Delta_i < 10$) or no support ($\Delta_i \geq 10$), with three models having larger Δi than the null model. The top three models received substantial weight of evidence (combined $w_i = 0.95$), with the best model having the largest weight ($w_i = 0.76$). All top models had good model fit at an alpha 0.001 level. The percentage deviance explained varied between the different models, with the largest amount of deviance explained by the best model (14.5%). The top three models had good predictive power and optimal probability cut-offs for these models were 50%.

The top models had intermediate complexity ($K_i = 6$, 5 and 7 respectively) (Table 5.2). Consumption sites were more likely to occur in areas used by ungulates, and models in which I replaced the ungulate variable with a species-specific variable (e.g., moose presence rather than overall ungulate presence) had lower fit than generic ungulate models, hence final models included pooled ungulates (Table 5.3). Models that included vertical cover had better fit than those in which vertical cover was replaced by stand basal area or forest age. Vertical cover and distance to nearest habitat edge were important predictors in two of the top three models, and in both cases consumption sites were more likely to occur in areas with high cover and close to edge.

Horizontal cover was an important predictor covariate in the top two models, although only for the second model the confidence interval for the coefficient estimate did not overlap zero. Distance to nearest trail was important in one top model, with consumption sites being more likely to occur away from trails. Distance to nearest stream was included in the third ranked model, but the confidence interval for its coefficient overlapped zero.

Caching and Kleptoparasitism

Bears cached ungulates at the majority (69.8%) of depredation sites, with the rest (30.2%) not having caches. Caches also were present at scavenging (84.1%) and unknown (58.8%) sites but because at these sites I was not always confident whether the bear or cougar had cached the prey, I did not include these in statistical testing. I did not locate multiple caches and in the rare (n = 4) cases where two ungulate carcasses were present at a site they had both been hidden in the same cache.

The bear that made the kill revisited the carcass the majority of the time (77.8%) whereas only 22.2% of ungulate carcasses were not revisited by predatory individuals. Carcasses were revisited regardless of whether they had been cached or not (logistic regression, Wald $\chi^2 = 1.03$, $df = 1$, $P = 0.31$) and with no clear relation to prey size (logistic regression, Wald $\chi^2 = 2.40$, $df = 1$, $P = 0.12$). Bears were not more likely to cache during the peak of ungulate resource use (calving/fawning/lambing season), leading to refuting of the resource-pulse hypothesis (Table 5.4). Also, bears were not likely to cache more to minimize meat spoilage, refuting the resource-spoilage hypothesis (Table 5.4). However bears were more likely to cache after killing a large-bodied ungulate (Table 5.5), thereby supporting the resource-size hypothesis for caching.

No model except the one describing the prey-size hypothesis received support, with unsupported models having larger Δ_i than the null model. The prey-size model received modest weight of evidence ($w_i = 0.43$) (Figure 5.4), and all other models had lower weight of evidence compared with the null model ($w_i = 0.28$) (Table 5.4). As shown by the goodness-of-fit Wald chi-square test, the prey-size model had good model fit at $\alpha = 0.05$ but explained only 4% of the deviance, had low predictive power (AUC = 0.57) and an optimal probability cut-off at 73%

(Table 5.5). This top model was univariate whereas five of the remaining six tested models were multivariate but with low complexity.

Cached and non-cached prey was detected by scavengers (logistic regression, Wald $\chi^2 = 0.65$, $df = 1$, $P = 0.42$) and 25.4% of ungulates depredated by grizzly bears were kleptoparasitised, primarily by coyotes (14.3%) and to a lesser extent by wolves (3.2%) and non-identified mammalian and avian predators (7.9%). Caches were more likely to be detected by scavengers if the cached prey was a large ungulate than if it were a smaller bodied ungulate (logistic regression, Wald $\chi^2 = 19.27$, $df = 1$, $P < 0.05$). Presence of scavengers at bear-depredation sites was associated with bears spending more time at the site (logistic regression, Wald $\chi^2 = 8.38$, $df = 1$, $P < 0.05$) possibly indicating that once kleptoparasites arrived at the site bears defended the carcass.

Use of Ungulates by Multiple Bears

Based on the radiocollar data I documented 16 instances of use of ungulate carcasses by multiple bears, representing 12.9% of my sample of carcass sites. In 15 of these instances, two bears used the carcass, whereas in one instance three different bears fed on an adult whitetail deer carcass. Of these instances, 9 involved use of a carcass by a male and a female, 6 involved use of a carcass by two females and one involved one male and two females. Only in two cases did two bears use the carcass concurrently, feeding on it simultaneously for 2 h and 5 h respectively, and both cases involved a male and a female. I did not document any use of the same carcass by two males or direct displacement of the first bear by the second bear. For bear depredation sites used by multiple bears ($n = 8$), the second bear arrived at the carcass 206.3 ± 136.3 h (*range* = 3−400 h) after the first bear. For scavenging sites used by multiple bears ($n = 6$), the second bear arrived at the carcass 216.83 ± 137.56 h (*range* = 42−390 h) after the first bear had started scavenging. There was no relationship between ungulate carcass size and number of hours until the second bear arrived at the site ($r = 0.187$, $df = 14$, $P = 0.49$) and the distribution of prey size weights did not differ for carcasses used by one or multiple bears (two-sample Wilcoxon rank-sum, $df_1 = 16$, $df_2 = 96$, $P = 0.31$).

DISCUSSION

Identifying habitat characteristics at locations where predators consume prey is important for managing declining populations of predator(s) and/or prey. In Alberta, increases in the extents of early seral stage habitats connected to industrial footprints can result in increased forage biomass and densities of elk (Visscher and Merrill 2009), moose (James et al. 2004), and deer (Latham et al. 2011b). In contrast, grizzly bears in the region are adversely affected by human activity which can result in habitat degradation and habitat sinks (Nielsen et al. 2004b, Nielsen et al. 2006). Because ungulates form an important part of grizzly bear diet in west-central Alberta (Munro et al. 2006), identification of habitats where bears consume ungulates can inform land-use planning to provide opportunities of energy gain for bears while minimizing risky encounters with humans. Models to predict ungulate consumption site distribution on the landscape (e.g., Nielsen et al. 2010) should strive to incorporate ecologically relevant ungulates such as elk, which has the highest proportion of occurrence in bear diet in my study area (Chapter 4), and also deer (Munro et al. 2006) in addition to moose. Such information can facilitate decisions that decrease mortality risk for bears, given that 90% of recorded grizzly bear mortalities are human-related and as many as 100% occur within 500 m of roads or 200 m of trails (Benn and Herrero 2002). In addition to facilitating conflict prevention, understanding behaviour of grizzly bears at ungulate kill sites allows insights into evolutionary adaptations and energetic trade-offs.

Grizzly bear choice of habitats for ungulate consumption has been poorly documented likely due to safety considerations and the difficulty of locating carcasses. Studies that have attempted to quantify habitat where bears consume ungulates have done so at the coarse scale of categorical habitat (Munro et al. 2006) or by recording percent forest cover (Mattson 1997, Nielsen et al. 2010) without testing multiple hypotheses on drivers of consumption site choice. In my study GPS radiotelemetry allowed precise identification of ungulate consumption sites and showed that grizzly bears did not consume ungulates at random landscape locations. Forested environments, primarily moderate and dense conifer with associated high vertical cover were chosen over more open environments for ungulate consumption, in accordance with Munro et al. (2006) and Nielsen et al. (2010). This finding highlights the importance of preserving forest patches when modifying landscapes such as through open-pit mining, because treed areas promote meat protein acquisition in this threatened bear population.

In the presence of wind, the odour plume emitted by a carcass will disperse, thereby increasing the chance of a scavenger encountering it (Ruzicka and Conover 2011). I found that ungulates were consumed in areas with high horizontal cover which decreases detection by visual scavengers and possibly by olfactory scavengers too, if cover provides shelter from wind. Numerous studies on felids have identified horizontal cover to be a key habitat feature for prey consumption sites in solitary carnivores such as cougars (Logan and Irwin 1985), Eurasian lynx (Podgorski et al. 2008), tigers (*Panthera tigris*) and leopards (*Panthera pardus*) (Karanth and Sunquist 2000). Dense undergrowth may decrease the movement rates of scavengers and consumption of carcasses in open areas increases kleptoparasitism (Gorini et al. 2011).

The observed patterns of ungulate consumption site choice do not support my predictions that sites would be located in areas where ungulates are less likely to be present. Conversely, ungulate carcasses were more likely to be located in areas where ungulates spent disproportionately more time (using pellet presence as proxy), close to streams and habitat edges. Distance to stream is an index of importance of riparian habitat (Bowyer et al. 1998) and in my study area richness of ground vegetation is negatively correlated with increased distance to stream areas ($r = -0.200$, $df = 888$, $P < 0.05$). Moose (Courtois et al. 2002) and deer (Laundre 2010) favour edges because of foraging opportunities, whereas elk can also use edges to trade off high diet quality in open areas away from edges for decreased predation risk from wolves near edges (Hernandez and Laundre 2005). In addition, edges can be perceived as secure by bears (Nielsen et al. 2004a), but they could also channel wind currents and enable faster detection by scavengers moving along edges.

The lack of support for models incorporating key bear plant foods suggests that carcass detection by other bears is likely not a factor in site choice in this low density grizzly bear population. Interestingly, human access along roads did not appear to influence choice of consumption sites, and I recorded scavenging events on hunter kills in the vicinity of roads. Many bears in my study area readily move near to roads or cross roads (Graham et al. 2010, Roever et al. 2010). However, consumption sites were more likely to be located far from trails, a potential mechanism to avoid detection by other predators or humans. Facultative scavengers including coyotes and wolves use trails for movements (Thornton et al. 2004, Latham et al. 2011a, McKenzie et al. 2012) because of fast displacement and decreased energetic cost along linear features.

Although I was interested in assessing habitat choice for ungulate consumption on reclaimed mines, I located only 14 carcasses within the disturbance limits of reclaimed mines, which precluded analyses by land designation. Reclaimed mines in my study area have forage for ungulates because wildlife habitat with emphasis on ungulates is a major end land-use objective for reclamation of open pit coal mines in Alberta (MacCallum 2005). The small number of carcasses on mines is likely connected to the relatively small proportion overlap of bear home ranges with reclaimed mines (0.24 ± 0.15, $n = 7$ bears) (Appendix 1).

Choice of habitats for minimizing scavenger presence did not appear to be an effective strategy for concealing prey and grizzly bears spent considerable time at large carcasses presumably defending them from scavengers. Because they are not territorial, bears do not need to leave the carcass to scent mark and actively defend territorial boundaries as done by other carnivores (Shivik and Young 2006, Powell 2012). Even when carcasses were cached, kleptoparasites detected them at a rate of 25.4%. Bears thus employ a dual strategy for minimizing loss to scavengers: defense and caching, and most likely a combination of the two. Although grizzly bears spend on average >19 hours at ungulate carcasses, I am uncertain of the interactions occurring at carcass locations. Unlike bears, cougars kill coyotes while defending carcasses (Koehler and Hornocker 1991). The lack of kleptoparasite kills at ungulate carcasses used by bears suggests that grizzlies may lack effective lethal mechanisms to avoid interference competition, although bears will defend carcasses from humans (Herrero and Higgins 2003).

In severe environments that have variable productivity and inconsistent availability of food, resource pulses can trigger caching behaviour (Orland and Kelt 2007, Careau et al. 2008). I did not find evidence for the resource-pulse hypothesis for caching by grizzly bears, potentially because of rapid consumption of small prey consumed during the calving season. However, young of the year calves were not always entirely consumed by bears and were still kelptoparasitised by scavengers despite being cached, unlike what Garneau et al. (2007) suggested. Depredated larger ungulates were more likely to be cached than smaller ones, which supports the prey-size hypothesis. For ungulates that were scavenged by bears I found no relationship between time bears spent at carcasses and carcass size, likely because carcasses had already been partially depleted by the predator(s) responsible for the kill.

Caching is more common in temperate than in tropical regions, because food spoilage in the latter works against caching efficiency (Smith and Reichman 1984). In temperate regions, cougars cache at low elevation where temperatures are higher (Bischoff-Mattson and Mattson 2009). Caching may be influenced by site humidity, because moisture favours microbial activity but also might increase detection by olfactory predators (Smith and Reichman 1984), given that scent travels better under moist conditions (Conover 2007). However I found no evidence for the resource-spoilage hypothesis, possibly because of rapid consumption times (before food spoilage) or insensitivity to spoiled food.

I likely underestimated inter-specific kleptoparasitism rate because I used scavenger scat as an index of kleptoparasitism occurrence. A less-persistent kleptoparasite that detected and fed on the carcass before being chased away by a returning bear might not have spent enough time or eaten enough food to trigger scat deposition. I attempted to standardize detectability by including only those sites with <25% snow cover and intensively searching all sites for scavenger scat, including using shovels to dig under snow when present.

The presence of certain scavengers could be explained by one specific pilferer strategy, which is to follow storers and try to kleptoporasitize cached food (Grodzinski and Clayton 2010). Ravens (*Corvus corax*) can follow large carnivores (Stahler et al. 2002), black-backed jackals (*Canis mesomelas*) follow leopards (Bothma 1998), and coyotes may be following grizzly bears in the same way they follow wolves to wolf-killed ungulates (Paquet 1991). Because of the small size of bird droppings, I likely underestimated avian scavengers at ungulate carcasses used by grizzly bears. Remote cameras set at two opportunistically encountered fresh carcasses registered scavenging ravens, eagles, jays and coyotes, with coyotes observed at five additional ungulate carcasses. These chance observations support my scat-based coyote presence data at bear-used carcasses, suggesting that coyotes may be the most common mammalian scavengers in the region.

Meat subsidy to other bears through reciprocal pilferage (Vander Wall and Jenkins 2003) also plays a role in energetic loss and gain. Reciprocal pilfering may resemble cooperative behaviour but is in reality driven by individual selfishness (Grodzinski and Clayton 2010). While small solitary animals with overlapping home ranges may be able to tolerate high rates of pilfering, the large body size of adult grizzly bears and ability to daily ingest ungulate meat at a biomass of up to 8% of their own body weight (Hilderbrand et al. 1999a) suggest bears may not be able to sustain high pilfering. In my study only 12.9% of carcasses were used by more than one bear and 75% of intra-specific pilferage occurred during the 2.5 month-long brown bear mating season (Steyaert et al.

2012). I did not document displacement of a bear by another bear at carcass sites, but because I did not radiocollar the entire population of grizzly bears, these observations should be interpreted with caution given that I found >1 adult bear bed at 35.8% of 67 ungulate consumption sites that had beds visible.

Many animals have adaptations for caching (Smith and Reichman 1984). In grizzly bears, it has been speculated that the long claws and large shoulder muscles are adaptations for digging roots, tubers and rodents (Herrero 1978), although not as effective as those of other species specializing in scratch digging (Mattson 1998). Because digging is energetically costly (Vleck 1979), bears likely compensate behaviourally by digging when rewards are high (Mattson 2004), such as is the case when caching ungulate carcasses. Additional energetic loss could occur if a bear drags killed prey to concealed areas, but because of timing of field visitation under logistical and safety constraints and typical absence of snow cover I was not able to reliably identify drag marks.

In birds it has been suggested that social species that cache are better at locating caches than solitary species that cache or than non-caching social species (Grodzinski and Clayton 2010). In carnivorous mammals, further understanding of the relation between predator sociobiology and fluctuation in need for caching through space use and territoriality (Smith and Reichman 1984) will help improve estimates of prey partitioning and provide insights into how these factors impact kill and scavenging rates. In addition, future work could investigate the role of seasonality in habitat choice for consumption sites, monitor behaviour at the cache site, more accurately quantify kleptoparasitism and compare habitat choice, caching and rates of pilferage of caches in simple systems with those in areas with multiple obligate and facultative scavengers, where subsidies to scavengers might be more complex.

LITERATURE CITED

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

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. Journal of Wildlife Management **64**:912-923.

Ashenafi, Z. T., T. Coulson, C. Sillero-Zubiri, and N. Leader-Williams. 2005. Behaviour and ecology of the Ethiopian wolf (*Canis simensis*) in a human-dominated landscape outside protected areas. Animal Conservation **8**:113-121.

Barker, O. E., and A. E. Derocher. 2009. Brown bear (*Ursus arctos*) predation of broad whitefish (*Coregonus nasus*) in the Mackenzie Delta Region, Northwest Territories. Arctic **62**:312-316.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry **64**:691-692.

Benn, B., and S. Herrero. 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971-98. Ursus **13**:213-221.

Bischoff-Mattson, Z., and D. Mattson. 2009. Effects of simulated mountain lion caching on decomposition of ungulate carcasses. Western North American Naturalist **69**:343-350.

Bothma, J. D. 1998. A review of the ecology of the southern Kalahari leopard. Transactions of the Royal Society of South Africa **53**:257-266.

Boulanger, J., G. B. Stenhouse, M. Proctor, S. Himmer, D. Paetkau, and J. Cranston. 2005. 2004 Population inventory and density estimates for the Alberta 3B and 4B Grizzly bear management area. Report prepared for Alberta Sustainable Resource Development, Fish and Wildlife Division. Integrated Ecological Research, Nelson, BC, Canada.

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

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

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

Careau, V., J. F. Giroux, and D. Berteaux. 2007. Cache and carry: hoarding behavior of arctic fox. Behavioral Ecology and Sociobiology **62**:87-96.

Careau, V., N. Lecomte, J. Bety, J. F. Giroux, G. Gauthier, and D. Berteaux. 2008. Hoarding of pulsed resources: Temporal variations in egg-caching by arctic fox. Ecoscience **15**:268-276.

Caro, T., and P. W. Sherman. 2011. Endangered species and a threatened discipline: behavioural ecology. Trends in Ecology and Evolution **26**:111-118.

Cattet, M., J. Boulanger, G. Stenhouse, R. A. Powell, and M. L. Reynolds-Hogland. 2008. An evaluation of long-term capture effects in ursids: Implications for wildlife welfare and research. Journal of Mammalogy **89**:973-990.

Chatterjee, S., and A. S. Hadi. 2006. Regression analysis by example. John Wiley & Sons, Inc., Hoboken, NJ, USA.

Conover, M. R. 2007. Predator and prey dynamics: The role of olfaction. Taylor & Francis, Boca Raton, FL, USA.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. Ecology **80**:566-575.

Courtois, R., C. Dussault, F. Potvin, and G. Daigle. 2002. Habitat selection by moose (*Alces alces*) in clear-cut landscapes. Alces **38**:177-192.

Craighead, L. 2000. Bears of the world. MBI Publishing Company, St. Paul, MN, USA.

Davidson, A. D., M. J. Hamilton, A. G. Boyer, J. H. Brown, and G. Ceballos. 2009. Multiple ecological pathways to extinction in mammals.

Proceedings of the National Academy of Sciences, USA **106**:10702-10705.

Elgmork, K. R. 1982. Caching behavior of brown bears (*Ursus arctos*). Journal of Mammalogy **63**:607-612.

Finke, D. L., and W. E. Snyder. 2010. Conserving the benefits of predator biodiversity. Biological Conservation **143**:2260-2269.

FMF. 2007. Protocol for the capture, handling, and sampling of grizzly bears. Foothills Model Forest Grizzly Bear Research Program, Hinton, AB, Canada.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**:11. [online] URL: http://www.consecol.org/vol6/iss1/art11

Garneau, D. E., E. Post, T. Boudreau, M. Keech, and P. Valkenburg. 2007. Spatio-temporal patterns of predation among three sympatric predators in a single-prey system. Wildlife Biology **13**:186-194.

Gittleman, J. L., S. M. Funk, D. Macdonald, and R. K. Wayne. 2001. Carnivore conservation. Cambridge University Press, Cambridge, UK.

Gorini, L., J. D. C. Linnell, R. May, M. Panzacchi, L. Boitani, M. Odden, and E. B. Nilsen. 2011. Habitat heterogeneity and mammalian predator–prey interactions. Mammal Review **42**:55-77.

Graham, K., J. Boulanger, J. Duval, and G. Stenhouse. 2010. Spatial and temporal use of roads by grizzly bears in west-central Alberta. Ursus **21**:43-56.

Grodzinski, U., and N. S. Clayton. 2010. Problems faced by food-caching corvids and the evolution of cognitive solutions. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:977-987.

Harrison, S. 1990. Cougar predation on bighorn sheep in the Junction Wildlife Managemen Area, British Columbia. M.S. Thesis. University of British Columbia, Vancouver, BC, Canada.

Henry, S. E., M. G. Raphael, and L. F. Ruggiero. 1990. Food caching and handling by marten. Great Basin Naturalist **50**:381-383.

Hernandez, A. 1995. Temporal-spatial patterns of food caching in 2 sympatric shrike species. Condor **97**:1002-1010.

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

Herrero, S. 1978. Comparison of some features of evolution, ecology and behavior of black and grizzly-brown bears. Carnivore **1**:7-17.

Herrero, S., and A. Higgins. 2003. Human injuries inflicted by bears in Alberta: 1960-98. Ursus **14**:44-54.

Hilderbrand, G. V., S. G. Jenkins, C. C. Schwartz, T. A. Hanley, and C. T. Robbins. 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Canadian Journal of Zoology **77**:1623-1630.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999b. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology **77**:132-138.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist **91**:385-398.

Honer, O. P., B. Wachter, M. L. East, and H. Hofer. 2002. The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. Journal of Animal Ecology **71**:236-246.

Huber, P. J. 1967. The behavior of maximum likelihood estimates under non-standard conditions. In: Proceedings of the Fifth Berkeley symposium on mathematical statistics and probability. University of California Press, Berkeley, CA, USA.

Jacoby, M. E., G. V. Hilderbrand, C. Servheen, C. C. Schwartz, S. M. Arthur, T. A. Hanley, C. T. Robbins, and R. Michener. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management **63**:921-929.

James, A. R. C., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management **68**:799-809.

Karanth, K. U., and M. E. Sunquist. 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. Journal of Zoology **250**:255-265.

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat selection studies. Journal of Wildlife Management **68**:774-789.

Kissui, B. M. 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Animal Conservation **11**:422-432.

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.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010a. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management **74**:1435-1447.

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

Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. Journal of Mammalogy **72**:391-396.

Kolowski, J. M., and K. E. Holekamp. 2009. Ecological and anthropogenic influences on space use by spotted hyaenas. Journal of Zoology **277**:23-36.

Koppel, J. V. d., R. D. Bardgett, J. Bengtsson, C. Rodriguez-Barrueco, M. Rietkerk, M. J. Wassen, and V. Wolters. 2005. The effects of spatial scale on trophic interactions. Ecosystems **8**:801-807.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience **54**:123-138.

Lanszki, J., M. Molnar, and T. Molnar. 2006. Factors affecting the predation of otter (*Lutra lutra*) on European pond turtle (*Emys orbicularis*). Journal of Zoology **270**:219-226.

Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecological Applications **21**:2854-2865.

Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011b. Invading white-tailed deer change wolf-caribou dynamics in Northeastern Alberta. Journal of Wildlife Management **75**:204-212.

Laundre, J. W. 2010. Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. Ecology **91**:2995-3007.

Laundre, J. W., and L. Hernandez. 2003. Winter hunting habitat of pumas *Puma concolor* in northwestern Utah and southern Idaho, USA. Wildlife Biology **9**:123-129.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science **2**:314-320.

Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography **28**:385-393.

Logan, K. A., and L. L. Irwin. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. Wildlife Society Bulletin **13**:257-262.

MacCallum, B. 2005. Reclamation of wildlife habitat in Alberta's Foothills. Bighorn Environmental Design. In: Fish, fur and feather. Fish and wildlife conservation in Alberta: 1905-2005.The Fish and Wildlife Historical Society and the Federation of Alberta Naturalists, Altona, MB, Canada.

Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology **38**:921-931.

Marshal, J. P., P. R. Krausman, C. B. Vernon, S. S. Rosenstock, and W. B. Ballard. 2006. Gradients of forage biomass and ungulate use near wildlife water developments. Wildlife Society Bulletin **34**:620-626.

Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears - *Ursus arctos*. Biological Conservation **81**:161-177.

Mattson, D. J. 1998. Diet and morphology of extant and recently extinct northern bears. Ursus **10**:479-496.

Mattson, D. J. 2004. Exploitation of pocket gophers and their food caches by grizzly bears. Journal of Mammalogy **85**:731-742.

Mattson, D. J., and T. Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850 –2000. Conservation Biology **16**:1123-1136.

McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter predator movement and the functional response. Interface Focus **2**:205-216.

Merkle, J. A., D. R. Stahler, and D. W. Smith. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology **87**:56-63.

Merrill, E., H. k. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair. 2010. Building a mechanistic understanding of predation with GPS-based movement data. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2279-2288.

Michener, G. R. 2000. Caching of Richardson's ground squirrels by North American badgers. Journal of Mammalogy **81**:1106-1117.

Mitchell, M. S., and M. Hebblewhite. 2012. Carnivore habitat ecology: integrating theory and application. In eds. L. Boitani, and R. Powell:

Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, UK.

Mowat, G., and D. C. Heard. 2006. Major components of grizzly bear diet across North America. Canadian Journal of Zoology **84**:473-489.

Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy **87**:1112-1121.

Nielsen, S. E., and A. Haney. 1998. Gradient responses for understory species in a bracken grassland and northern dry forest ecosystem of Northeast Wisconsin. Transactions of the Wisconsin Academy of Sciences Arts and Letters **86**:149-166.

Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: Taking autocorrelation seriously. Ursus **13**:45-56.

Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience **10**:1-10.

Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004a. Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management **199**:51-65.

Nielsen, S. E., S. Herrero, M. S. Boyce, R. D. Mace, B. Benn, M. L. Gibeau, and S. Jevons. 2004b. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biological Conservation **120**:101-113.

Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation **130**:217-229.

Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation **143**:1623-1634.

Northrup, J. M., and M. S. Boyce. 2012. Mad cow policy and management of grizzly bear incidents. Wildlife Society Bulletin **36**:499-505.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin **5**:113-117.

Orland, M. C., and D. A. Kelt. 2007. Response of a heteromyid rodent community to larege- and small-scale resource pulses: Diversity, abundance, and home-range dynamics. Journal of Mammalogy **88**:1280-1287.

Paquet, P. C. 1991. Winter spatial relationships of wolves and coyotes in Riding-Mountain-National-Park, Manitoba. Journal of Mammalogy **72**:397-401.

Podgorski, T., K. Schmidt, R. Kowalczyk, and A. Gulczynska. 2008. Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriologica **53**:97-110.

Powell, R. A. 2012. Movements, home ranges, activity, and dispersal. In eds. L. Boitani, and R. A. Powell: Carnivore ecology and conservaton. A handbook of techniques. Oxford University Press, Oxford, UK.

Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology **68**:1645-1651.

Proctor, M. F., D. Paetkau, B. N. McLellan, G. B. Stenhouse, K. C. Kendall, R. D. Mace, W. F. Kasworm, C. Servheen, C. L. Lausen, M. L. Gibeau, W. L. Wakkinen, M. A. Haroldson, G. Mowat, C. D. Apps, L. M. Ciarniello, R. M. R. Barclay, M. S. Boyce, C. C. Schwartz, and C. Strobeck. 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. Wildlife Monographs **180**:1-46.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience **59**:779-791.

Quigley, H., and S. Herrero. 2005. Characterization and prevention of attacks on humans. In eds. R. Woodroofe, S. Thirgood, and A. Rabinowitz: People and wildlife: Conflict or coexistence. Cambridge University Press, Cambridge, UK.

Reader, T. 2003. Strong interactions between species of phytophagous fly: a case of intraguild kleptoparasitism. Oikos **103**:101.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters **12**:982-998.

Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step selection functions. Ecography **33**:1113-1122.

Ruth, T. K., P. C. Buotte, and H. B. Quigley. 2010. Comparing ground telemetry and Global Positioning System methods to determine cougar kill rates. Journal of Wildlife Management **74**:1122-1133.

Ruzicka, R. E., and M. R. Conover. 2011. Does weather or site characteristics influence the ability of scavengers to locate food? Ethology **118**:187-196.

Schwab, C., B. Cristescu, M. S. Boyce, G. B. Stenhouse, and M. Ganzle. 2009. Bacterial populations and metabolites in the feces of free roaming and captive grizzly bears. Canadian Journal of Microbiology **55**:1335-1346.

Shivik, J. A., and J. K. Young. 2006. What carnivore biologists can learn from bugs, birds, and beavers: a review of spatial theories. Canadian Journal of Zoology **84**:1703-1711.

Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology **12**:564-575.

Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics **15**:329-351.

Stahler, D., B. Heinrich, and D. Smith. 2002. Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. Animal Behaviour **64**:283-290.

Steyaert, S. M. J. G., A. Endrestol, K. Hacklaender, J. E. Swenson, and A. Zedrosser. 2012. The mating system of the brown bear *Ursus arctos*. Mammal Review **42**:12-34.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science **240**:1285-1293.

Thornton, D. H., M. E. Sunquist, and M. B. Main. 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in South-central Florida. Journal of Mammalogy **85**:973-982.

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

Valeix, M., G. Hemson, A. J. Loveridge, G. Mills, and D. W. Macdonald. 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. Journal of Applied Ecology **49**:73-81.

Vander Wall, S. B., and S. H. Jenkins. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. Behavioral Ecology **14**:656-667.

Visscher, D. R., and E. H. Merrill. 2009. Temporal dynamics of forage succession for elk at two scales: Implications of forest management. Forest Ecology and Management **257**:96-106.

Vleck, D. 1979. Energy-cost of burrowing by the pocket gopher *Thomomys bottae*. Physiological Zoology **52**:122-136.

Wasser, S. K., B. Davenport, E. R. Ramage, K. E. Hunt, M. Parker, C. Clarke, and G. Stenhouse. 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. Canadian Journal of Zoology **82**:475-492.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10**:964-976.

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.

Weber, W., and A. Rabinowitz. 1996. A global perspective on large carnivore conservation. Conservation Biology **10**:1046-1054.

White, H. 1982. Maximum-likelihood estimation of mis-specified models. Econometrica **50**:1-25.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003a. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology **72**:909.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003b. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters **6**:996-1003.

Winterbach, H. E. K., C. W. Winterbach, M. J. Somers, and M. W. Hayward. 2012. Key factors and related principles in the conservation of large African carnivores. Mammal Review. Online Early doi: 10.1111/j.1365-2907.2011.00209.x.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science **280**:2126-2128.

Wright, J. D., and J. Ernst. 2004. Wolverine, *Gulo gulo luscus*, resting sites and caching behavior in the boreal forest. Canadian Field-Naturalist **118**:61-64.

Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. Ursus **17**:95-108.

Table 5.1: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for a categorical habitat model describing the probability of sites where grizzly bears consume ungulates in west-central Alberta, Canada. Estimates for which the [CI] did not overlap zero are given in bold. Model fit, predictive power and cut-off probability also are reported.

Variable		β_i	Robust SE	95% CI Lower	95% CI Upper
Habitat class					
	Shrub	0.944	0.757	−0.539	2.428
	Mixed forest	1.318	1.382	−1.390	4.026
	Open conifer	0.930	0.608	−0.262	2.122
	Moderate conifer	**1.671**	**0.691**	**0.317**	**3.026**
	Dense conifer	**1.690**	**0.636**	**0.444**	**2.936**
Model eval.		χ^2	df	*P*	
	Wald test	24.33	5	<0.001	
	ROC (AUC)	0.65			
	Cut-off probab.	0.50			

Pooled barren land and herbaceous land classes were withheld as a reference category.

Table 5.2: Model structure and deviance for candidate models (RSFs) describing habitat at sites where grizzly bears consume ungulates in west-central Alberta, Canada. Model assessment was done by ranking AIC_c values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. Models are presented in decreasing ranking order, with the top model given in bold. Models with Δ_i larger than the null model are at the bottom of the list.

Hypotheses	**Variables**	K_i	**-2LL**	**% Dev. explained**	AIC_c	Δ_i	w_i
UNG + DET	**Ungulate + V cover + H cover + Dist edge + Dist edge^2**	**6**	**146.9**	**14.5**	**161.4**	**0.0**	**0.76**
UNG + DET	Ungulate + H cover + Dist trail + Dist trail^2	5	153.3	10.8	165.0	3.6	0.13
UNG	Ungulate + V cover + Dist edge + Dist edge^2 + Dist stream + Dist stream^2	7	149.0	13.3	166.4	5.0	0.06
DET.H	V cover + H cover + Dist road + Dist road^2 + Dist trail + Dist trail^2	7	151.9	11.6	169.3	7.9	0.01
UNG + DET.B	Ungulate + Herb + Root + Berry	5	158.3	7.9	170.0	8.6	0.01
UNG + DET	Ungulate + V cover + H cover + Dist edge + Dist edge^2 + Dist trail + Dist trail^2	8	149.6	13.0	170.1	8.7	0.01
UNG	Ungulate	2	166.9	2.9	171.2	9.8	0.01
UNG	Ungulate + Dist edge + Dist edge^2	4	162.6	5.4	171.7	10.4	0.00
UNG + DET	Ungulate + Dist edge + Dist edge^2 + Dist trail + Dist trail^2	6	158.9	7.6	173.4	12.0	0.00
Null		1	171.9	0.0	174.0	12.6	0.00
UNG + DET.B	Ungulate + Herb + Root + Berry + Dist edge + Dist edge^2 + Dist stream + Dist stream^2	9	152.2	11.4	176.0	14.7	0.00
UNG + DET.B	Ungulate + Herb + Root + Berry + Dist road + Dist road^2 + Dist trail + Dist trail^2	9	154.3	10.3	178.1	16.7	0.00
DET.H	Dist road + Dist road^2 + Dist trail + Dist trail^2	5	167.6	2.5	179.3	18.0	0.00

UNG - Ungulate; DET - Detection by scavengers, including bears and other predator species; DET.B - Detection by bears; DET.H - Detection by humans

% Dev. explained - percentage deviance explained

Table 5.3: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for the top 3 models describing the probability of occurrence for grizzly bear ungulate consumption sites in west-central Alberta, Canada as assessed by Δ_i and w_i. Models 1 and 2 are ungulate and detection models whereas model 3 is an ungulate model. Estimates for which the [CI] did not overlap zero are given in bold. Model fit, predictive power and cut-off probability also are reported.

		Model 1				**Model 2**				**Model 3**			
Variable		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
				Lower	Upper			Lower	Upper			Lower	Upper
Ungulate													
	Ungulate	**0.524**	**0.237**	**0.059**	**0.990**	**0.656**	**0.241**	**0.184**	**1.128**	**0.544**	**0.197**	**0.158**	**0.930**
	V cover	**0.014**	**0.005**	**0.004**	**0.025**					**0.018**	**0.006**	**0.006**	**0.030**
	Dist edge	**−0.021**	**0.005**	**−0.031**	**−0.010**					**−0.022**	**0.005**	**−0.321**	**0.012**
	Dist edge^2	**0.000**	**0.000**	**0.000**	**0.000**					**0.000**	**0.000**	**0.000**	**0.000**
	Dist stream									−0.001	0.002	−0.004	0.002
	Dist stream^2									0.000	0.000	−0.000	0.000
Detection													
	H cover	0.177	0.100	-0.018	0.372	**0.302**	**0.110**	**0.087**	**0.518**				
	Dist trail					**0.005**	**0.001**	**0.003**	**0.008**				
	Dist trail^2					−0.000	0.000	−0.000	0.000				
Model eval.		χ^2	df	*P*		χ^2	df	*P*		χ^2	df	*P*	
	Wald test	29.18	5	<0.001		24.09	4	<0.001		53.36	6	<0.001	
	ROC (AUC)	0.74				0.72				0.73			
	Cut-off probab.	0.50				0.50				0.50			

Table 5.4: Model structure and deviance for candidate models describing multiple hypotheses for presence/absence of a cache at grizzly bear depredation sites on ungulates in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. Models are presented in decreasing ranking order, with the top model given in bold. Models with Δ_i larger than the null model are at the bottom of the list.

Hypotheses	**Variables**	K_i	**-2LL**	**% Dev. explained**	**AIC$_c$**	Δ_i	w_i
R.SIZE	**Prey size**	**2**	**74.1**	**4.0**	**78.4**	**0.0**	**0.43**
Null		1	77.1	0.0	79.2	0.9	0.28
R.SIZE + R.PULSE	Prey size + Peak neonates	3	74.1	4.0	80.7	2.3	0.14
R.PULSE	Peak neonates	2	77.0	0.1	81.4	3.0	0.10
R.SPOILAGE	V cover + SSI + Elevation	4	75.5	2.2	84.6	6.2	0.02
R.SIZE + R.SPOILAGE	Prey size + V cover + SSI + Elevation	5	72.9	5.5	84.6	6.2	0.02
R.PULSE + R.SPOILAGE	Peak neonates + V cover + SSI + Elevation	5	75.3	2.3	87.1	8.7	0.01
R.SIZE + R.PULSE + R.SPOILAGE	Prey size + Peak neonates + V cover + SSI + Elevation	6	72.9	5.5	87.4	9.0	0.00

R.SIZE - Resource (ungulate prey) size; R.PULSE - Resource pulse (peak in ungulate neonates); R.SPOILAGE - Resource spoilage; more likely at low vertical cover, high moisture (based on SSI - site severity index) and low elevation

% Dev. explained - percentage deviance explained

Table 5.5: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for top models describing the probability of cache presence at grizzly bear depredation sites in west-central Alberta, Canada as assessed by Δ_i and w_i. Estimates for which the [CI] did not overlap zero are given in bold. Model fit, predictive power and cut-off probability also are reported.

Variable		β_i	Robust SE	95% CI	
				Lower	Upper
Prey size		**0.012**	**0.005**	**0.002**	**0.023**
Model eval.		χ^2	df	*P*	
	Wald test	5.57	1	0.018	
	ROC (AUC)	0.57			
	Cut-off probab.	0.73			

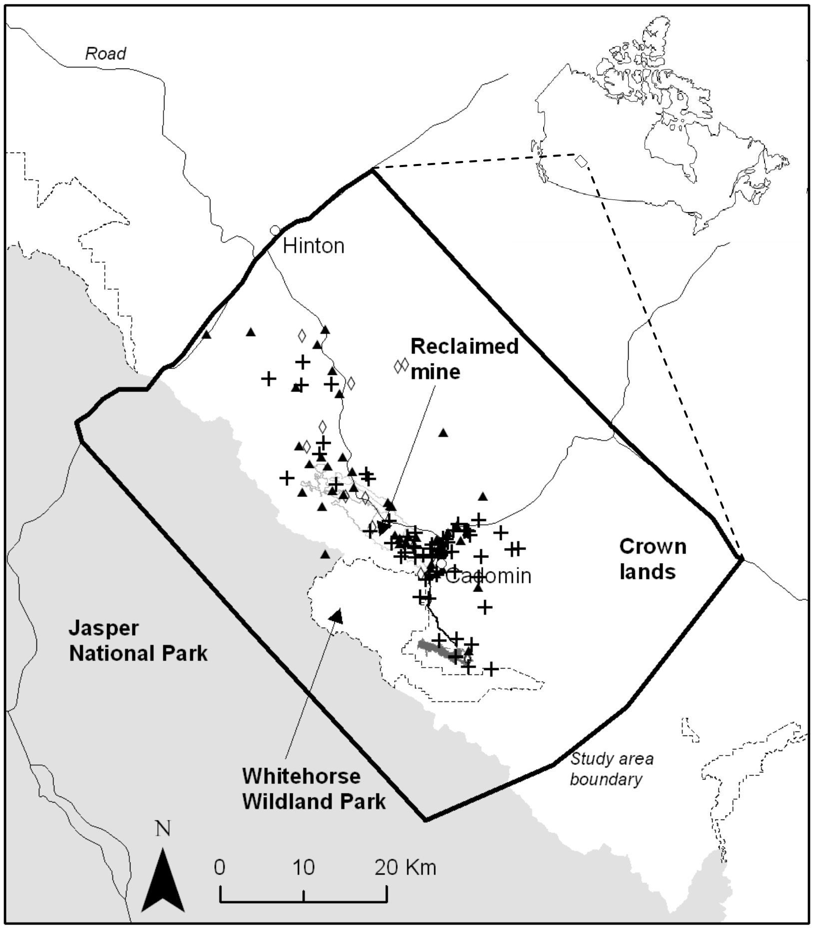

Figure 5.1: Study area for grizzly bear ungulate consumption in west-central Alberta, Canada, including major roads and colour coded land designations: Crown lands (white shading), protected areas (National park, light gray shading; Wildland Park, dashed black boundary), reclaimed mines (gray boundary) and active mine (dark gray shading). Crosses are grizzly bear depredation sites (n_1 = 63), black triangles are scavenging sites (n_2 = 44) and white diamonds are ungulate consumption sites of unknown origin (n_3 = 17), visited in the field in 2009 and 2010.

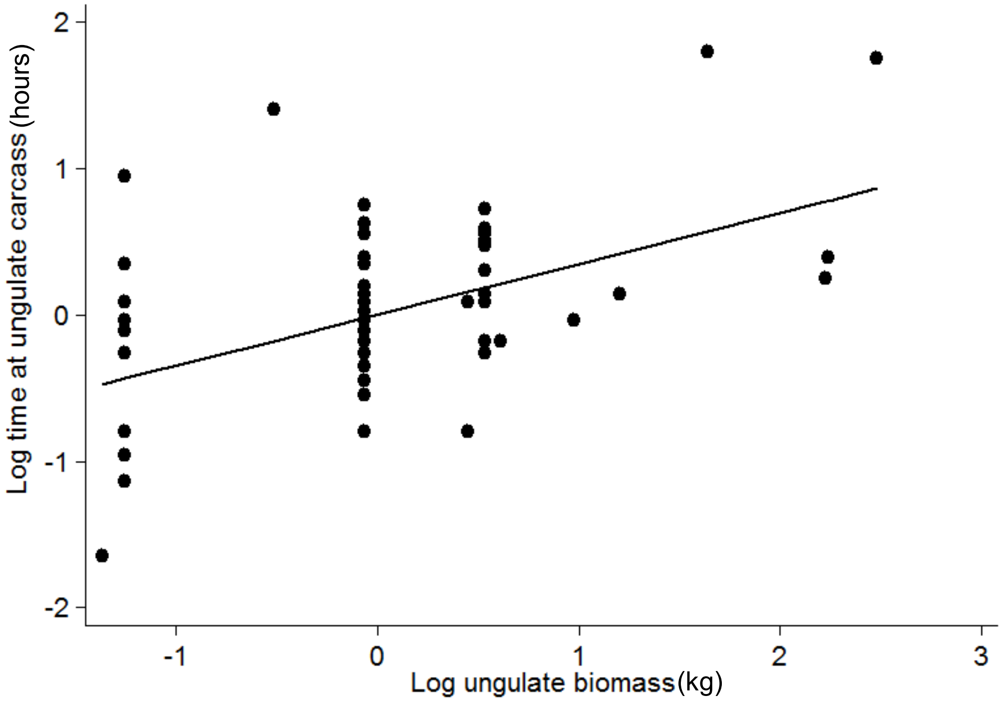

Figure 5.2: Time spent by predatory grizzly bears in west-central Alberta, Canada (2009-2010) at an ungulate carcass as a function of carcass size (*n* = 63 depredation sites).

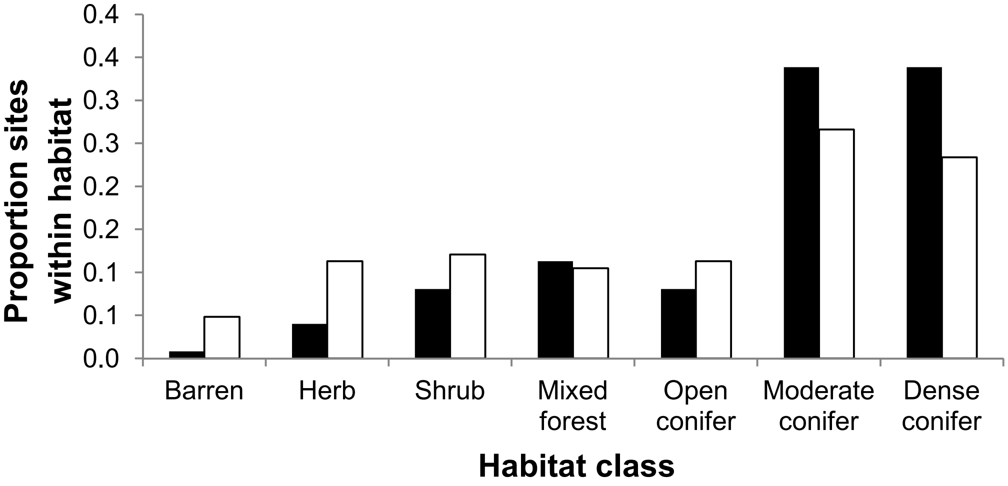

Figure 5.3: Habitat class at 124 sites where grizzly bears consumed ungulates and 124 random sites in west-central Alberta, Canada.

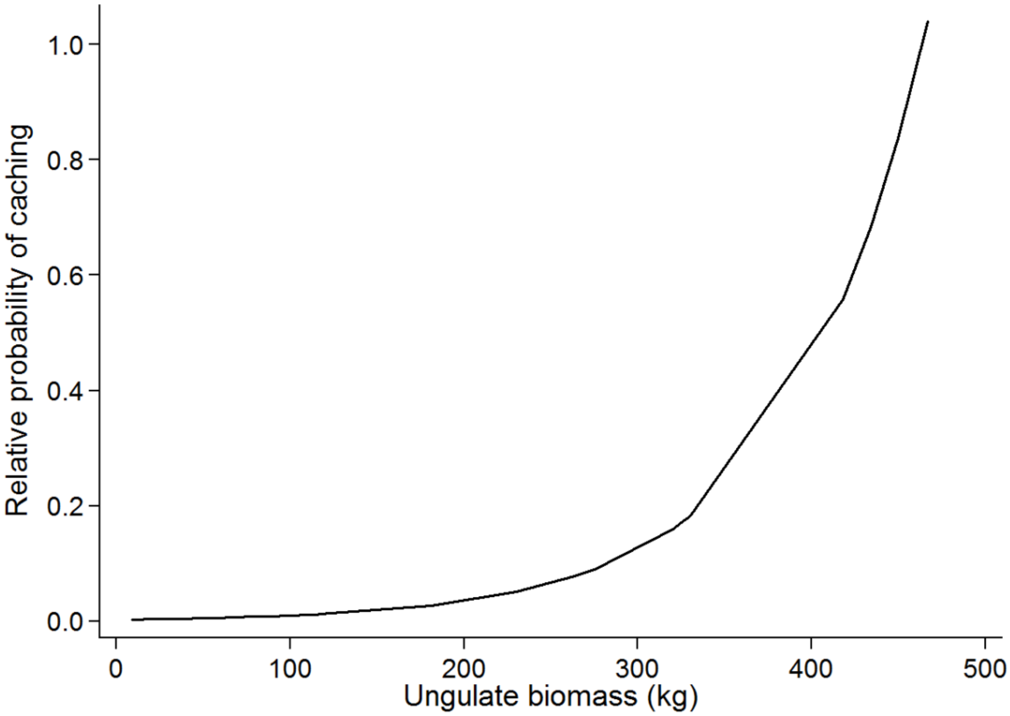

Figure 5.4: Relative probability of grizzly bear caching ungulate prey killed in west-central Alberta, Canada as a function of prey size (*n* = 63 depredation sites), based on the univariate prey size model with cache presence/absence as dependent variable.

CHAPTER 6

PERCEPTION OF HUMAN-DERIVED RISK INFLUENCES CHOICE AT TOP OF THE FOOD CHAIN

ABSTRACT

On landscapes where humans are present, wildlife behaviour is a trade-off between maximizing fitness and minimizing human-derived risk. Understanding risk perception in wildlife can bring mechanistic insights that allow mitigation of anthropogenic risk factors, with benefits to long-term animal fitness. Areas where animals choose to rest should minimize risk from predators, which for large facultative or obligate carnivores typically equate to humans. I hypothesize that high human activity leads to selection for habitat security, whereas low human activity is perceived as safer, thereby carnivores in low human use areas should trade security for forage. To test these predictions, I investigated selection of resting (bedding) sites by GPS radiocollared adult grizzly bears (n = 10) sampled from a low density population in a multi-use landscape in Alberta, Canada. I compared security and foods at resting and random locations while accounting for land use, season, and time of day. Bears selected areas with high horizontal cover and far from trails for resting on reclaimed mines with low human access, but did not avoid open (herbaceous) areas, with resting occurring primarily at night. In protected areas bears also bedded at night and bedding sites were associated with berry shrubs and *Hedysarum* spp. roots, with horizontal cover selected in the summer, when human recreation is highest. On public lands where human recreation was substantial, bears bedded at day, selected resting sites with high horizontal cover in the summer and proximity to habitat edges, with bedding associated with herbaceous foods. These spatial and temporal patterns of selection suggest that bears perceive human-related risk differentially in relation to human activity level, season and time of day, and employ a security-food trade-off strategy. Although grizzly bears are presently not hunted in Alberta, their perceived risks associated with humans influence resting-site selection.

INTRODUCTION

Where wildlife and humans coexist, animals can modify their behaviour compared to areas without human use, and anticipating these behavioural changes can benefit wildlife conservation (Anthony and Blumstein 2000, Caro 2007, Stankowich 2008). Proactive understanding of animal behavioural response to humans is important particularly for large carnivore species sharing landscapes with human populations, because the major cause of mortality in many carnivores is conflict with people (Woodroffe and Ginsberg 1998, Woodroffe 2000, Treves and Karanth 2003). Carnivore response to human activity can be seen as analogous with prey response to predation risk (Frid and Dill 2002) or spatial dynamics within predator guilds. During periods of wolf presence, elk (*Cervus elaphus*) use steeper slopes and have greater sinuousity in movements (Laporte et al. 2010) whereas African ungulates avoid habitats where they are likely to be depredated (Thaker et al. 2011). Cougars (*Puma concolor*) avoid typical use areas during periods of wolf (*Canis lupus*) use (Kortello et al. 2007) and the most reproductively successful female cheetahs (*Acinonyx jubatus*) are found near areas with low lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*) densities (Durant 2000).

Fear of predation has thus led to the evolution of antipredator strategies based primarily on associating environmental features (i.e., habitat characteristics) and adaptive strategies for coping with predation risk (Boissy 1995). For example, prey species can reduce perceived risk and fear through evolving adaptive behaviours (Stankowich and Blumstein 2005) such as choosing resting sites that offer cover (*sensu* Mysterud and Ostbye [1999]) thus minimizing the risk of detection. To minimize risk, resting sites often are located in sheltered areas, such as roe deer (*Capreolus capreolus*) fawns bedding in forest patches (Linnell et al. 1999) and elk resting in low-use wolf areas (Frair et al. 2005). Shifting habitats to densely forested areas may decrease risk of predation by cursorial predators but increase vulnerability to stalking predators (Atwood et al. 2009). Dense cover might thus have an opposite effect from that desired by the prey, by decreasing detectability of an approaching predator (Gorini et al. 2011) and may be particularly ineffective at eluding olfactory predators (Conover 2007). An additional complication is that selecting areas with perceived low predation risk, while reducing direct effects, can have detrimental consequences to fitness through an increase in risk effects, such as by sacrificing the amount of time spent in food-rich areas (Creel and Christianson 2008). Still, because risk effects carry less cost than direct predation (Creel and Christianson 2008), selection for low predation risk is employed to maximize survival, but a risk-reward trade-off is likely operating in animal decision making.

Perceived predation risk from humans might be higher for unpredictable human activity occurring at irregular time intervals, such as recreation (Miller et al. 2001), although human use of trails could be more predictable than random use of the landscape (Whittaker and Knight 1998). Seasonally high levels of recreation (summer) may thus elicit differences in carnivore response to humans. At a finer temporal scale and particularly when displacement may not be an option because of habitat limitations or territoriality mechanisms, periods when humans are most active (day-time) may coincide with periods of low carnivore mobility/resting (McLellan and Shackleton 1988, Gibeau et al. 2002) with secure habitat influencing resting-site selection (Ordiz et al. 2011). Developing predictive models that possibly correlate with animal fear can improve understanding of carnivore and other wildlife response to human activity (Blumstein and Fernandez-Juricic 2004).

In addition to the detrimental effects of fear associated with predation risk, such as decrease in use of areas with adequate food sources, fitness also is influenced by ability to thermoregulate. Physiological comfort factors into resting-site selection (Van Moorter et al. 2009, Ordiz et al. 2011) but is difficult to monitor in field studies of wide ranging carnivores. However, canopy (hereafter, vertical cover) provides overhead thermal cover (Mysterud and Ostbye 1995) and insulation from atmospheric precipitation or direct sunlight. Because wind hitting an animal's body surface decreases bodily temperature through convective heat loss (Merrill 1991), visibility (hereafter, horizontal cover) at resting sites may affect thermoregulation, because sites with low visibility have surrounding habitat structures that provide wind shelter.

While accounting for the potential influence of thermal comfort, this study tested whether food, security or a combination of food and security determine choice of a facultative carnivore's resting (bedding) sites, and whether differences in risk perception (fear) result in selection of sites with different types of security and food features as a function of land use, season, and time of day. I used grizzly bears (*Ursus arctos*) in a complex landscape with different levels of human activity as a study system and defined 'bed' to be a spot where a bear rested, curling up on the substrate and leaving body prints or other discernible signs (Mysterud 1983). I focused exclusively on beds used during the bear active season, i.e. outside bear winter denning. My study organism is the largest North American terrestrial facultative carnivore that at its adult stage has no natural enemy except humans. As the least resilient large carnivore of the Rocky Mountains (Weaver et al. 1996), the grizzly bear has experienced a substantial range decline as a result of persecution by humans and habitat loss (Laliberte and Ripple 2004). In Alberta, Canada where this study was conducted the species was designated as Threatened in 2010 because of low population estimates for the province with more than 90% of grizzly bear mortalities on record being human-caused (Benn and Herrero 2002). Human access is an important predictor in models describing relative mortality risk of Alberta grizzly bears (Nielsen et al. 2004a).

European brown bears respond to increase in risk of mortality during the legal hunting season by selecting areas with dense cover (Ordiz et al. 2011). In Alberta, grizzly bear hunting is no longer allowed but human activity is on the rise in bear habitat and includes open-pit mining, logging, oil and gas development and recreation (Nielsen et al. 2004a). Recreation is the most unpredictable of these activities and supported by an extensive network of unpaved roads and trails that facilitate human access in bear habitat on Crown (public) lands (Nielsen et al. 2006). In contrast, on reclaimed open-pit mines human access is restricted to a few designated trails, whereas in protected areas human access also is minimal.

Based on this variation in human access by land designation, I predict that in choosing resting sites grizzly bears perceive protected areas and reclaimed mines as secure because of low human use of these areas. Given the low presence of humans as well as high energy gain requirements to sustain a large body mass, I predict that the primary driver of resting-site selection in protected areas and on reclaimed mines is food. In contrast, I predict that when on Crown lands where there is high human access, bears will select areas far from people, with high cover, steep slopes and close to edge. Seasonally, I predict that bears will seek more concealment during summer because of high levels of human recreation but not during fall because human access is lower and restricted primarily to hunters, and no hunting of grizzly bears is allowed in Alberta. In regards to time of day, I expect that bears seek more cover while resting during day-time when humans are active on the landscape.

METHODS

Study Area

We performed the study in a 3,200 km^2 area that encompassed Rocky Mountains and foothills of west-central Alberta, Canada (Figure 6.1). The western part of the area is mountainous, whereas the eastern part includes a hilly region with gentler slopes. Coniferous forest dominates the landscape and includes white (*Picea glauca*), black (*P. mariana*) and Engelmann (*P. engelmannii*) spruce, lodgepole pine (*Pinus contorta*), balsam (*Abies balasamea*) and subalpine (*A. lasiocarpa*) fir. Mixed and deciduous forest types occur at lower elevations and on sunny south facing slopes, being composed primarily of trembling aspen (*Populus tremuloides*) and balsam polar (*P. balsamifera*). Main grizzly bear foods are sweet vetch roots (*Hedysarum* spp.), herbaceous forbs and monocots, berries, and ungulates including moose (*Alces alces*), elk (*Cervus elaphus*), deer (*Odocoileus virginianus* and *O. hemionus*) and bighorn sheep (*Ovis canadensis*).

Crown land is mainly found in the eastern sector of the study area, and hosts open-pit mining for coal, forest harvesting, oil and gas exploitation and extensive recreation (All Terrain Vehicles, hunting, horseback riding, mountain biking, hiking and camping). The western sector is primarily protected provincially (Whitehorse Wildland Park) and federally (Jasper National Park), with one operational mine and a cement quarry operating in the area. The community of Cadomin (population = 60) is the only permanent settlement. Two neighbouring reclaimed mines are located at the centre of the study area, one completely and the second largely reclaimed. The northern area boundary is a major paved highway, and the region has extensive roads and trails on Crown lands which are heavily used by recreationists.

Data Collection

Adult grizzly bears were captured and radiocollared in spring/early summer and fall 2009 and 2010 with assistance from the Foothills Research Institute Grizzly Bear Program, using protocols approved by the University of Alberta and University of Saskatchewan Animal Care and Use Committees. Capture methods included culvert trapping, helicopter darting and limited leg-hold snaring (Cattet et al. 2008), with captures performed on public land, mine sites, and a Wildland Park to avoid capture-induced bias by method or land designation. Remotely downloadable GPS radiocollars (Telus UHF; Followit, Lindesberg, Sweden) were programmed to acquire a location every hour during the bear-active season (March 15-December 1). Only 20% of monitored bears did not have GPS radiocollar locations on reclaimed mines, 30% did not have locations in protected areas, and all bears had locations on Crown lands.

Individual bears were approached monthly on the ground or from aircraft to download data remotely from their radiocollars, while maintaining >200 m distance to minimize disturbance. Field visitation occurred for a sample of GPS location clusters, as identified with a clustering algorithm modified from Knopff et al. (2009) to include 1-h GPS fix inputs and 50 m distance between the two initial points in a cluster. An attempt was made to visit the largest four clusters for each bear during each month and randomly other clusters, thereby keeping sampling effort consistent between individul bears. Cluster sites were located based on centroids included in the algorithm output, which were transferred to hand-held GPS units. Crews accessed sites on foot or via truck, ATV or helicopter and searched a 50 m radius from the centroid for all evidence of bear activity fitting the cluster date. Visitation occurred 41 ± 15 days after the first fix in the cluster because of care not to distrub the animal, safety, and logistical constraints.

A bed-site consisted of a depression excavated by the bear or a resting event occurring on a natural substrate contour. Even when excavations were located, only sites at which I confirmed the presence of multiple bear hairs in the bed and/or attached to the bark/branches of adjacent tree(s) were classified as bedding sites and included in analyses. Often such sites had multiple bear scats. Once the bed was located, I delineated a 20×20-m plot centred on the bed-site (or on a randomly chosen bed if >1 beds were detected) and performed a habitat survey within the plot. Sampling was replicated at a plot 300 m away on one of 4 cardinal directions from the confirmed resting site, with clockwise choice of subsequent directions (N, E, S and W respectively).

Elevation was recorded from a barometric altimeter on the GPS unit and slope and aspect were recorded with a compass equipped with a clinometer. I classified each site as barren land (<5% vegetated), herbaceous (>5% vegetated, <5% shrub cover, <5% tree cc), shrub (>5% shrub cover, <5% tree cc), mixed forest (21-79% conifer), open conifer (5-30% cc, >80% conifer), moderate conifer (31-69% cc, >80% conifer) or dense conifer (>70% cc, >80% conifer). Nine plots in regenerating coniferous forest were reclassified as open, moderate or dense conifer based on vertical cover. I recorded percentage vertical cover for the site using a spherical densiometer (Lemmon 1956), averaging 4 readings (one in each cardinal direction) at each of 5 quadrant locations on a north-south transect through the plot centre. I noted vertical cover for the bed-site and overall plot average. I assessed horizontal cover at the bed and 1 m from the ground using a foldable sheet with two 50×30.48 cm alternating red and white rectangles, adapting the method of Nudds (1977). One crew member stood in the bed-site holding the sheet vertically and the second technician averaged two readings taken from north and south and 10 m away. A 2-m factor prism was used at treed plots to estimate stand basal area for live and dead trees separately. Forest age was estimated visually as immature, mature or old. Using a diameter-breast-height (dbh) tape I measured the diameter (cm) of the two largest trees in the plot and the diameter of the largest tree on a radius of 1.5 m from the bed.

I recorded percentages cover for nine forb and legume species as well as pooled monocots consumed by grizzly bears in the region (Nielsen et al. 2003, Munro et al. 2006), using five 0.7×0.7-m quadrants distributed at 5 m intervals along the north-south transect through the plot centre. Because of concerns with differential plants growth in the time since the bear had been at the site, I derived presence/absence data from percentage cover. Monocots were excluded from analyses because of their omni-presence at the sites (90%). The presence/absence of eleven berry shrubs used by grizzly bears in the area (Nielsen et al. 2003, Nielsen et al. 2010) was recorded in the quadrants separately. I also recorded species-specific presence of ungulate pellet groups within the 20×20-m plot, but pulled data across species because of increased model fit. When snow was present, I still recorded ground vegetation after clearing the snow from quadrants. I accounted for differential detectability of ungulate pellets by recording snow cover in four percentage classes, and only sites with <25% snow cover were included in analyses.

Based on 2-m resolution colour orthoimagery and field knowledge, I used ArcMap v.9.2 (ESRI, Redlands, California) to measure the Euclidean distance from the bed (centre of the plot) to the nearest river/stream, road, trail and habitat edge, defined as the border between two habitat classes as classified above. Although vertical cover, horizontal cover and elevation recorded at the site all drive a site's microclimate, I further accounted for physiological requirements of a resting bear by deriving the Nielsen and Haney (1998) site-severity index (SSI) modified from the Beer's aspect transformation (Beers et al. 1966). The index incorporates slope and aspect providing a measure of solar insulation and moisture, northeast slopes having the lowest solar insulation and highest moisture (low index values) and southwest slopes having the highest solar insulation and xeric moisture (high index values).

Modeling Grizzly Bear Resting Habitat

Resting-Site Selection

I used discrete choice models (Cooper and Millspaugh 1999) based on conditional logistic regression to identify variables influencing selection of resting sites at the scale of bear mean hourly step length. I applied a matched-case design with one random site associated with each resting site as a trade-off between sampling availability and maximizing number of resting sites visited. The random location (0) was conditioned to occur 300 m away from the location selected for resting (1). The 300 m distance between the resting site and the paired random site incorporates knowledge of the movement rates of adult bears in my study system (annual mean step length 269 m/h outside winter denning, range 175–367, based on 11 adult bears monitored in the area prior to this study). Even though use-availability designs are often appropriate in wildlife habitat studies (Johnson et al. 2006), I assumed a matched-case design with 0% contamination (*sensu* Keating and Cherry [2004]) and found no evidence of bear resting at any paired location sampled away from cluster sites. In addition, the large number of sites available for resting on the landscape suggests that future bedding at sites I defined as random is unlikely.

Because I was interested in differences in bear resting-site selection in areas with different levels of human activity, I performed separate analyses for each land designation defined as: 1. reclaimed mine with minimal recreational access restricted to designated trails; 2. protected area with minimal human use

(Whitehorse Wildland Park and Jasper National Park); 3. public land with high levels of recreation (Crown lands). I created three sets of *a priori* resting-site selection models for each land designation based on my understanding of bear biology and hypothesized bear response to human activity. The first set included food models with forage covariates exclusively, the second set included models of perceived security with no food covariates and the final set included models that combined food and percseived security covariates. I excluded highly correlated variables (Pearson correlation $|r| > 0.6$) from all candidate models and assessed potential collinearity between linear predictors using variance inflation factors (VIF) diagnostics. Variables with individual VIF scores >10 or the mean of all VIF scores substantially larger than 1 were collinear and not used in the same model (Chatterjee and Hadi 2006). I thus dropped stand basal area and forest age because they were highly correlated between themselves and with vertical cover. I also excluded the habitat categorical habitat classification because of high correlations with vertical cover, and ran a distinct conditional logistic regression analysis to estimate selection coefficients for each habitat class.

I tested the effects of squared terms on model performance and included such terms for distance to road, trail and edge. Distance to edge is typically considered a food variable for ungulate distribution modelling, but I included it as a security variable in candidate models for grizzly bear resting-site selection because edges serve security functions for this species (Nielsen et al. 2004b). Robust standard errors were computed to control for heteroskedasticity and minimize bias in parameter estimation for all models.

I used ΔAICc (small sample size correction for AIC) and AICc weights to determine top models (Burnham and Anderson 1998, Anderson et al. 2000) for each land designation and every model set (food, security, food + security). The top three models (four if the weights for two models were identical) from each set were included in a second and similar model selection procedure which ranked competing food, security and food + security models. Following Boyce et al. (2002), I used Area Under the Curve (AUC) to assess the predictive power of top models, and sensitivity and specificity to derive the optimal probability cut-off for assigning presence-absence of a resting site (Liu et al. 2005).

Influence of Non-Habitat Factors on Resting-site Selection

I identified three factors that could influence patterns of resting-site selection by bears: land designation, season and time of day. Land designation followed the classification described above. Following Nielsen et al. (2004b) and my first and last field confirmed bedding event, I divided my data into three seasons: “hypophagia” (spring; April 21 to June 14), “early hyperphagia” (summer; June 15 to August 7) and “late hyperphagia” (fall; August 8 to October 28), and pooled data across the two years of monitoring. Time of day (period) when resting commenced was classified as diurnal (sunrise to sunset), crepuscular (morning twilight to sunrise and sunset to evening twilight) and nocturnal (evening twilight to morning twilight) time periods. I used sunrise, sunset and civil twilight tables (http://www.cmpsolv.com/los/sunset.html, accessed October 17, 2011) based on expected conditions for the centre of my study area (Cadomin, Alberta, Canada; 53°N, 117°20'W) in the Mountain Time zone. I assessed whether bears rested more at certain times of day by performing chi-square tests for each land designation.

I used generalized linear models (GLM; Gaussian family) with maximum likelihood optimization to investigate the effects of the three factors on all four variables that significantly influenced resting-site selection, as identified from the resting-site selection models: vertical and horizontal cover, distance to edge and distance to trail. I included the three non-habitat factors and interaction terms in candidate models following calculation of Pearson correlation coefficients between predictor variables and VIF diagnostics at above specified cut-offs. To incorporate habitat availability, dependent variables were inputted as ratios calculated by dividing the habitat value at each resting site by the value at each associated random site. For example, the value for vertical cover on top of a given bed-site was divided by the value for vertical cover at the paired random site.

Prior to inclusion in models, all dependent variables were log-transformed to obtain Gaussian distributions. The model took the form

$$\log(\frac{X_u}{X_r}) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_k X_k$$

where X_u is the value for the habitat variable of interest (e.g., vertical cover) recorded at the resting site, X_r is the value for the same habitat variable at the paired random site, β_0 is the intercept, and β_1 to β_k are estimated GLM coefficients for predictor variables X_1 to X_k. I used robust standard errors to further control for imperfect normality and heteroskedasticity. I ranked candidate models using ΔAICc and AICc weights which allowed identification of the top model for each of the dependent variable investigated. For all four best models I plotted standardized Pearson and deviance residuals, inspected the residuals for normality and used the Pregibon leverage statistic (Pregibon 1981) to identify potential observations that influenced coefficient sensitivity. I re-ran the models without these observations and checked for differences in coefficient estimation. Individual observations and combinations of these had little influence on regression output.

Within-plot Resting-Site Selection

By within-plot selection I refer to selection of habitat features at the micro-scale (within the 20×20-m field-delineated plot). For all sites where resting was confirmed by field visitation, I compared mean vertical cover on top of the bed with mean vertical cover for the plot using Wilcoxon matched-pairs signed-ranks tests as the data did not follow a Gaussian distribution. I used the same type of test to assess whether the distribution of bedding trees (defined as the largest standing dbh tree on a radius on 1.5 m from the bed) was similar to the distribution of the largest or second largest dbh tree in the 20×20-m plot respectively. The latter analysis was carried out only for sites that had at least one tree (*n* = 242). The null hypothesis of each test was that the distributions under comparison were the same.

RESULTS

In 2009 and 2010, I captured and deployed GPS radiocollars on 12 adult grizzly bears in the study area. Two large males slipped off the collars within a month of capture and were not considered for analyses. The remaining bears included 6 females and 4 males I monitored for 383 bear-days during hypophagia (mean 7.1 bears), 683 bear-days in early hyperphagia (mean 12.6 bears) and 640 bear-days in late hyperphagia (mean 7.8 bears). During May-November 2009 and 2010 I located a total of 279 bedding sites 19% of which were found on reclaimed mines, 14% in protected areas and 67% on Crown lands (Table 6.1). The 50 m radius search performed at each GPS location cluster revealed that regardless of land designation most sites had a single bear bed; reclaimed mine had the highest proportion of single beds (1.04 ± 0.19 beds/site) followed by protected areas (1.21 ± 0.57 beds/site) and Crown lands (1.28 ± 0.72 beds/site).

Resting-Site Selection

Bears avoided barren land for resting regardless of land designation (Table 6.2, Figure 6.2). When on reclaimed mines, bears selected open conifer forest for resting, a habitat class little represented on mines and composed of regenerating conifer trees. When in protected areas and Crown lands, bears had negative selection for resting in the herbaceous land class. The strongest response to habitat class was on Crown lands, where bears not only avoided open habitats (barren and herbaceous) when choosing resting sites, but also selected against more concealed habitats such as open conifer and shrub, when compared to dense conifer. As shown by the goodness-of-fit Wald chi-square test results, the habitat class models were significant and with good predictive power (reclaimed mines: AUC = 0.73; protected areas: AUC = 0.87) except for the Crown land model (AUC = 0.68). Optimal probability cut-offs were 50% for all three models.

Of the 36 candidate models tested for each land designation (9 food models; 14 security models; 13 combined food and security models), only the top model for reclaimed mines had substantial support ($\Delta_i < 2$) (Table 6.3). In comparison, three models for protected areas (Table 6.4) and three models for Crown lands (Table 6.5) received substantial support. Security and combined food and security models had varying amount of support whereas food models had essentially no support ($\Delta_i > 10$). The top model for reclaimed mines ($w_i = 0.49$) was a model with security variables only. The top model for protected areas ($w_i = 0.37$) was a combined food and security model, with the second and third ranked models having security variables only. The top ($w_i = 0.40$) model for Crown land also was a combined food and security model, whereas the second and third ranked models included security variables only. Goodness-of-fit Wald chi-square tests revealed that all top bedding site selection models had good model fit at an alpha 0.01 level of significance (Table 6.6). The percentage deviance explained varied between the different models, with the largest amount of deviance explained by the best models for resting on reclaimed mines (42.9%) and protected areas (43.5%) whereas the Crown land model accounted for 19.1% of the deviance. The models for reclaimed mines and protected areas had high predictive power (reclaimed mine: AUC = 0.91; protected area: AUC = 0.90) and the Crown land model had good predictive power (AUC = 0.78). For all top models, optimal probability cut-offs were close to 50%.

The top models were complex for reclaimed mines ($K_i = 8$) and Crown lands ($K_i = 7$) whereas the protected-area top model had an intermediate number of parameters ($K_i = 5$) (Table 6.6). Irrespective of land designation, vertical cover and, with one exception, horizontal cover, were present in all models that received substantial support. Bears selected areas with high vertical cover when resting in protected areas and on Crown land but did not select vertical cover for bedding on reclaimed mines (Figure 6.3). When resting on reclaimed mines and Crown lands, they selected strongly for high horizontal cover but there was no strong selection when in protected areas (Figure 6.4). Distance to edge was a variable in all models for reclaimed mines and Crown land that received substantial support but was absent from all best models for protected areas. Bears selected areas close to edge when bedding on Crown land. When selecting resting sites on reclaimed mines, bears avoided areas near human access trails but distance to trail was absent from best models for protected areas and Crown lands. Presence/absence of berries was a variable in the best model for protected areas but the confidence interval for the coefficient estimate overlapped zero. Presence/absence of herbaceous foods was a variable in the best Crown lands model but the confidence interval for the coefficient estimate also overlapped zero. Slope and elevation were absent from all best models but slope was present in the third ranked model for Crown land. Regardless of land designation, sites selected for resting were drier and more exposed to solar insulation (high severity index values) compared to random sites, however the confidence intervals did overlap zero in all cases.

Influence of Non-habitat Factors on Resting-Site Selection

When on reclaimed mines, bears were most likely to rest at night and relatively equally likely to rest during the day and at crepuscular times ($\chi^2 = 8.1$, $df = 2$, $P = 0.017$) (Figure 6.5). In protected areas, bears were most likely to rest at night and least likely to rest during crepuscular times ($\chi^2 = 8.8$, $df = 2$, $P = 0.012$). On Crown lands, bears were most likely to rest during the day and least likely to rest during crepuscular times ($\chi^2 = 55.04$, $df = 2$, $P < 0.0001$).

Our variable combinations for season, land designation and time of day were adequate at explaining selection ratios for bear resting. The best models of a suite of 10 candidate models ranked for each of four selection ratios are presented in Table 6.7. The models for vertical and horizontal cover selection ratios were the only ones for which the coefficients did not overlap zero, therefore I report the estimates from the top models for these two factors only (Table 6.8), with estimates for all cover models reported in Table S.1. Of the 10 candidate models that influenced selection of vertical and horizontal canopy cover respectively, only the top candidate models had substantial support ($\Delta_i > 2$) while the remaining models had no support ($\Delta_i > 10$). The top models had a disproportionate weight of evidence compared to the competing models (vertical cover model: $w_i = 1.00$;

horizontal cover model: w_i = 0.99). Both models were complex (K_i = 4) and included the same set of parameters which were land designation, season and an interaction term between land designation and season. Bears selected against vertical cover when choosing resting sites in protected areas in the fall. They also selected sites with more horizontal cover when resting in protected areas and on Crown lands during summer.

Only two candidate models testing the influence of non-habitat factors on distance to edge selection ratio had substantial support. Both models included land designation and time of day, with the better model also including an interaction term (model with interaction: w_i = 0.49; simpler model: w_i = 0.37). The distance to trail selection ratio models had poor fit, with only one model having greater weight than the corresponding null model (best model: w_i = 0.22; null: w_i = 0.19).

Within-plot Resting-Site Selection

Given an alpha level of 0.1, vertical cover at resting sites located on reclaimed mines differed between the actual bed and mean vertical cover for the 20×20-m plot at the centre of which the bed was located (Wilcoxon matched-pairs signed-ranks test, z = 1.90, P = 0.06). Vertical cover on top of the bed differed substantially from the mean vertical cover for the plot for protected areas (Wilcoxon matched-pairs signed-ranks test, z = 4.3, $P < 0.0001$) and Crown lands (Wilcoxon matched-pairs signed-ranks test, z = 6.7, $P < 0.0001$), with the higher cover on top of the bed.

The nearest tree on a radius of 1.5 m from the bed was not likely to be the largest dbh tree in the 20×20-m plot irrespective of whether the bed site was located on a reclaimed mine (Wilcoxon matched-pairs signed-ranks test, z = 4.0, $P < 0.0001$), protected area (Wilcoxon matched-pairs signed-ranks test, z = 4.2, $P < 0.0001$) or Crown land (Wilcoxon matched-pairs signed-ranks test, z = 10.6, $P < 0.0001$). It also was not likely to be the second largest dbh tree whether on a reclaimed mine (Wilcoxon matched-pairs signed-ranks test, z = 3.9, $P < 0.0001$), protected area (Wilcoxon matched-pairs signed-ranks test, $z = 2.3$, $P = 0.02$) or Crown land (Wilcoxon matched-pairs signed-ranks test, $z = 7.6$, $P < 0.0001$).

DISCUSSION

While it is widely recognized that protecting vast areas of habitat is key for the long-term persistence of large carnivore populations, expansion of human activities into carnivore habitat increases the potential for conflict with humans (Woodroffe and Ginsberg 1998, Kolowski and Holekamp 2006, Smith et al. 2010). Herein I related recreational human activities according to land designation, season and time of day to the behavioural choice of a facultative carnivore's resting habitat selection and found differential selection associated with variation in perceived human-related risk. Selection of resting sites is in itself an adaptation for decreasing risk (Creel and Christianson 2008), thereby providing insights into risk perception in wild carnivores. When asleep, animals cannot use evolutionary mechanisms of coping with risky situations, such as long-distance perception of danger through scent, sight or hearing, flight response, dominance displays or aggressive physical contact. Therefore, in the vulnerable state of resting, animals rely on their choice of a secure bedding site for minimizing risk and maximizing survival probability. Security (horizontal cover) appears to be a key component in choice of resting sites by carnivores such as Eurasian lynx (Podgorski et al. 2008) and Florida panther (Comiskey et al. 2002), and high vertical cover is an excellent predictor of fisher resting-site selection (Zielinski et al. 2004, Purcell et al. 2009).

Grizzly bears have evolved in predominantly open environments with the large body size serving as a protection against possible aggressors (Stirling and Derocher 1990). However, during periods of unpredictable and intrusive human activity, for example bear hunting season, brown bears in Scandinavia select areas far from humans that also provide high concealment (Ordiz et al. 2011). Such selection might be an example of adaptive trait compensation (*sensu* [Dewitt et al. 1999]) in which the hiding strategy in the adaptive behaviour of avoiding 'predation' by hunters compensates for uselessness of morphological defences during resting. In contrast, grizzly bears in Alberta are currently protected from hunting so I did not expect strong selection for secure habitats during fall (ungulate hunting season) because human activity levels in the fall are low compared to summer. I expected variation in resting-site selection by land designation in relation to differential human access.

Although habitat on reclaimed mines was likely secure because of restricted human access, I found that bears perceived reclaimed mines as relatively insecure, selecting horizontal cover and avoiding areas close to trails for bedding. However, there was no selection against herbaceous areas (Table 6.2) and 48% of beds on mines were in open grasslands characteristic of reclaimed mines. Herbaceous areas on mines generally have high horizontal cover because grasses and forbs sown as part of reclamation can reach ~1 m height at maturity. Furthermore, 52% of resting events commenced at night (Figure 6.5), suggesting that perceived risk while on reclaimed mines did not induce major changes in the expected normal behavioural patterns of grizzly bears (bedding at night). My finding of bears resting in herbaceous areas contrasts with the findings of Mysterud (1983) for brown bears in Scandinavia and an earlier study of grizzly bears in my study area (Munro et al. 2006). In the latter study the probability of bear resting in herbaceous areas was zero. The strong avoidance of trails is surprising given the overall low levels of human access and may be indicative of negative past experiences or detection of people from far distances because of habitat openness.

Bears perceived protected areas as secure, with vertical cover being the only variable for habitat security included in the best resting-site selection model. Vertical cover may be more indicative of thermal comfort than affording security (Mysterud and Ostbye 1995) and the best model included an association of resting sites with presence of berry shrubs. Although I found no influence of trails on resting-site selection, the GLM model for horizontal cover selection ratio showed that bears select horizontal cover in the summer, which is the season when human access in protected areas is the highest. Interestingly, in the fall bears select bedding sites in areas with low vertical cover. I believe that this pattern relates to the distribution of foods consumed by bears at that time of year. In areas below 1,700 m elevation *Hedysarum* spp. roots are the primary food consumed in my study area starting late September (Munro et al. 2006) and presence of roots at fall sites in protected areas had a slight negative correlation with vertical cover ($r = -0.22$). This suggests a potential trade-off of body heat loss when being exposed to fall atmospheric precipitation while resting versus energetic gain of being present where the food is and avoiding energy loss when travelling through snow. I do not think that bedding where food is present exposes bears to high risk of intra-specific competition because bear density in the area is low (Boulanger et al. 2005).

Although I expected avoidance of areas close to trails and roads on Crown lands, distances to these linear human access features were not included in top models. Because of the widespread network of trails and roads on Crown lands and high use of these linear features by humans, bears inhabit a landscape where the presence of human recreation is a reality to be accepted. The association between bear resting sites on Crown lands and presence of herbaceous foods supports previous research showing that on public lands bears select areas close to roads to graze on plants such as clover (*Trifolium* spp.) (Roever et al. 2008). Bears in my study area move close to roads throughout the day (Roever et al. 2010), a pattern which contrasts with the daytime road avoidance by grizzly bears inhabiting an area of intensive resource extraction (McLellan and Shackleton 1988), and with bears in mountainous areas with limited human use having an inverse response to access compared to those in an area with high human use (Ciarniello et al. 2007). I demonstrated that roads and trails do not influence resting-site selection by bears on Crown lands, but bears select sites with high horizontal cover and close to habitat edge for resting in these high human-use areas.

Bears bedded more at daytime on Crown lands, indicating a temporal mechanism of avoiding people, but I cannot reach the same conclusion as the

Mace et al. (1996) study where bears became negatively conditioned to human activity, temporally and spatially avoiding high human-use areas. A similar pattern of temporal avoidance of humans was found for grizzly bears in the Bow Valley of Alberta avoiding trails during the human active period (Gibeau et al. 2002). The temporal avoidance mechanism does show that although herbaceous foods are present at bear resting sites on Crown land, this land designation is still perceived as risky, a finding which does not support the idea of habituation to people. While habituation of grizzly bears to hikers may alleviate human-bear conflict by reducing the risk of fear-induced charges (Jope 1985), on Crown lands in Alberta where many trail users carry firearms during the ungulate hunting season habituation might also expose bears to increased risk of mortality through illegal shooting.

My *a priori* expectation that bears would perceive risk differently in relation to levels of human activity was supported by the discrete choice models as well as by GLM analyses of selection ratios for four factors that promoted security, with all best models including land designation as a variable. Of the three land designations where resting sites were located, spatial avoidance of people (resting far from trails) was a factor only on reclaimed mines, whereas temporal avoidance came into play on Crown lands. Seasonal strong selection for horizontal cover during high human activity (summer and fall) corresponds to Scandinavian brown bear selection of high cover in summer and fall (Ordiz et al. 2011).

Previous studies have generalized the idea that resting sites are selected based on habitat security and there have been few attempts to assess the influence of food resources on where bedding events occur. I tested the effects of occurrence of major food items, cover, slope, elevation, distance to nearest road, trail and edge on bedding site selection and also incorporated a site severity index which improved model fit and accounted for physiological comfort required by bears. Although I monitored a substantial proportion of the grizzly bear population in the 3,200 km^2 study area (*n* = 10 adult bears, in an area with a population density of 4.79 bears/1,000 km^2 [Boulanger et al. 2005]), the results are based on pooled data across bear reproductive class, age and sex because of sampling limitations.

I found that although grizzly bear resting sites can be associated with the occurrence of major plant foods (berry shrubs, herbaceous forage and potentially *Hedysarum* spp. roots), food factors are not important predictors of choice of bedding sites. My results demonstrate that vertical and horizontal cover along with distance to trail and edge are important drivers of resting-site selection in grizzly bears. Mysterud (1983) and Mollohan (1987) also found cover to be an important factor in brown and black bear bedding-site selection, respectively. Slope, elevation and distance to road had poor predictive power in my study system which is in contrast with the findings that brown bear (Mysterud 1983) and black bear (Mollohan 1987) beds occur on steep slopes, at higher elevation and far from roads, although Mysterud (1983) did find that sheep-killing bears in Scandinavia did not avoid forestry roads for bedding. At the level of within-site selection, 76% of resting sites were associated with trees, a result which contrasts with grizzly bear resting sites in Yellowstone National Park where 87% of beds were within 1 m of a tree (Blanchard 1983), but resembles Scandinavian brown bear bedding sites 78% of which were associated with a tree (Mysterud 1983). Bedding trees were typically not large dbh trees, in contrast with trees at black bear (Mollohan 1987) and sun bear (Te Wong et al. 2004) bedding sites.

In my study system bears exhibit complex behavioural mechanisms to minimize perceived human-derived risk including selection for cover, edge, spatial avoidance of areas near trails and temporal avoidance of people for resting, depending on land designation and season. Although grizzly bears are not hunted in Alberta, the moratorium on grizzly bear hunting was introduced in 2006, only three years before my data collection and four years before the species was designated as Threatened. It is therefore possible that choice of resting sites by bears may be influenced by the 'ghost of predation past' (Peckarsky and Penton 1988), a proposition that has also been put forward for brown bear reproductive allocation (Zedrosser et al. 2011).

LITERATURE CITED

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. Journal of Wildlife Management **64**:912-923.

Anthony, L. L., and D. T. Blumstein. 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce Ne. Biological Conservation **95**:303-315.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial partitioning of predation risk in a multiple predator-multiple prey system. Journal of Wildlife Management **73**:876-884.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry **64**:691-&.

Benn, B., and S. Herrero. 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971-98. Ursus **13**:213-221.

Blanchard, B. M. 1983. Grizzly Bear: Habitat relationships in the Yellowstone area. Bears: Their Biology and Management **5**:118-123.

Blumstein, D. T., and E. Fernandez-Juricic. 2004. The emergence of conservation behavior. Conservation Biology **18**:1175-1177.

Boissy, A. 1995. Fear and fearfulness in animals. The Quarterly Review of Biology **70**:165-191.

Boulanger, J., G. B. Stenhouse, M. Proctor, S. Himmer, D. Paetkau, and J. Cranston. 2005. 2004 Population inventory and density estimates for the Alberta 3B and 4B Grizzly bear management area. Report prepared for Alberta Sustainable Resource Development, Fish and Wildlife Division. Integrated Ecological Research, Nelson, BC, Canada.

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

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

Caro, T. 2007. Behavior and conservation: a bridge too far? Trends in Ecology and Evolution **22**:394-400.

Cattet, M., J. Boulanger, G. Stenhouse, R. A. Powell, and M. L. Reynolds-Hogland. 2008. An evaluation of long-term capture effects in ursids: Implications for wildlife welfare and research. Journal of Mammalogy **89**:973-990.

Chatterjee, S., and A. S. Hadi. 2006. Regression analysis by example. John Wiley & Sons, Inc., Hoboken, NJ, USA.

Ciarniello, L. M., N. S. Boyce, D. C. Heard, and D. R. Seip. 2007. Components of grizzly bear habitat selection: Density, habitats, roads, and mortality risk. Journal of Wildlife Management **71**:1446-1457.

Comiskey, E. J., O. L. Bass, L. J. Gross, R. T. McBride, and R. Salinas. 2002. Panthers and forests in south Florida: An ecological perspective. Ecology and Society **6** [online] URL: http://consecol.org/vol6/iss1/art18

Conover, M. R. 2007. Predator-prey dynamics: the role of olfaction. Taylor & Francis, Boca Raton, FL, USA.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. Ecology **80**:566-575.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution **23**:194-201.

Dewitt, T. J., A. Sih, and J. A. Hucko. 1999. Trait compensation and cospecialization in a freshwater snail: size, shape and antipredator behaviour. Animal Behaviour **58**:397-407.

Durant, S. M. 2000. Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx jubatus*. Animal Behaviour **60**:121-130.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology **20**:273-287.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**:11. [online] URL: http://www.consecol.org/vol6/iss1/art11

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

Gorini, L., J. D. C. Linnell, R. May, M. Panzacchi, L. Boitani, M. Odden, and E. B. Nilsen. 2011. Habitat heterogeneity and mammalian predator–prey interactions. Mammal Review **42**:55-77.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. Journal of Wildlife Management **70**:347-357.

Jope, K. L. 1985. Implications of grizzly bear habituation to hikers. Wildlife Society Bulletin **13**:32-37.

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat selection studies. Journal of Wildlife Management **68**:774-789.

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.

Kolowski, J. M., and K. E. Holekamp. 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. Biological Conservation **128**:529-541.

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

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience **54**:123-138.

Laporte, I., T. B. Muhly, J. A. Pitt, M. Alexander, and M. Musiani. 2010. Effects of wolves on elk and cattle behaviors: Implications for livestock production and wolf conservation. PLoS ONE **5** e11954.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science **2**:314-320.

Linnell, J. D. C., P. Nijhuis, I. Teurlings, and R. Andersen. 1999. Selection of bed-sites by roe deer *Capreolus capreolus* fawns in a boreal forest landscape. Wildlife Biology **5**:225-231.

Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography **28**:385-393.

Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. Journal of Applied Ecology **33**:1395-1404.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht, The Netherlands.

McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries - Effects of roads on behavior, habitat use and demography. Journal of Applied Ecology **25**:451-460.

Merrill, E. H. 1991. Thermal constraints on use of cover types and activity time of elk. Applied Animal Behaviour Science **29**:251-267.

Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin **29**:124-132.

Mollohan, C. M. 1987. Characteristics of adult female black bear daybeds in Northern Arizona. Bears: Their Biology and Management **7**:145-149.

Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy **87**:1112-1121.

Mysterud, A., and E. Ostbye. 1995. Bed-site selection by European roe deer (*Capreolus capreolus*) in Southern Norway during winter. Canadian Journal of Zoology **73**:924-932.

Mysterud, A., and E. Ostbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin **27**:385-394.

Mysterud, I. 1983. Characteristics of summer beds of European brown bears in Norway. Bears: Their Biology and Management **5**:208-222.

Nielsen, S. E., and A. Haney. 1998. Gradient responses for understory species in a bracken grassland and northern dry forest ecosystem of Northeast Wisconsin. Transactions of the Wisconsin Academy of Sciences Arts and Letters **86**:149-166.

Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience **10**:1-10.

Nielsen, S. E., S. Herrero, M. S. Boyce, R. D. Mace, B. Benn, M. L. Gibeau, and S. Jevons. 2004a. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biological Conservation **120**:101-113.

Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004b. Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management **199**:51-65.

Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation **130**:217-229.

Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation **143**:1623-1634.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin **5**:113-117.

Ordiz, A., O.-G. Stoen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia **166**:59-67.

Peckarsky, B. L., and M. A. Penton. 1988. Why do *Ephemerella* nymphs scorpion posture - a ghost of predation past. Oikos **53**:185-193.

Podgorski, T., K. Schmidt, R. Kowalczyk, and A. Gulczynska. 2008. Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriologica **53**:97-110.

Pregibon, D. 1981. Logistic-regression diagnostics. Annals of Statistics **9**:705-724.

Purcell, K. L., A. K. Mazzoni, S. R. Mori, and B. B. Boroski. 2009. Resting structures and resting habitat of fishers in the southern Sierra Nevada, California. Forest Ecology and Management **258**:2696-2706.

Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2008. Grizzly bears and forestry - II: Grizzly bear habitat selection and conflicts with road placement. Forest Ecology and Management **256**:1262-1269.

Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step selection functions. Ecography **33**:1113-1122.

Smith, D. W., E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982-2004. Journal of Wildlife Management **74**:620-634.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation **141**:2159-2173.

Stankowich, T., and D. T. Blumstein. 2005. Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society B-Biological Sciences **272**:2627-2634.

Stirling, I., and A. E. Derocher. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. Bears: Their Biology and Management **8**:189-204.

Te Wong, S., C. W. Servheen, and L. Ambu. 2004. Home range, movement and activity patterns, and bedding sites of Malayan sun bears *Helarctos malayanus* in the Rainforest of Borneo. Biological Conservation **119**:169-181.

Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogden, S. M. Niemann, and R. Slotow. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology **92**:398-407.

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

Van Moorter, B., J.-M. Gaillard, P. D. McLoughlin, D. Delorme, F. Klein, and M. S. Boyce. 2009. Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. Oecologia **159**:669-678.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10**:964-976.

Whittaker, D., and R. L. Knight. 1998. Understanding wildlife responses to humans. Wildlife Society Bulletin **26**:312-317.

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

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science **280**:2126-2128.

Zedrosser, A., S. M. J. G. Steyaert, H. Gossow, and J. E. Swenson. 2011. Brown bear conservation and the ghost of persecution past. Biological Conservation **144**:2163-2170.

Zielinski, W. J., R. L. Truex, G. A. Schmidt, F. V. Schlexer, K. N. Schmidt, and R. H. Barrett. 2004. Resting habitat selection by fishers in California. Journal of Wildlife Management **68**:475-492.

Table 6.1: Adult grizzly bear resting sites confirmed during field visitation of GPS radiocollar location clusters in 2010 and 2011 in west-central Alberta, Canada.

	Reclaimed mine			**Protected area**			**Crown land**			
	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall	Total
Bedding sites (#)	10	37	5	9	4	26	47	64	77	279
Bears	*G23 G37 G111 G113* *G118* G112 G115			*G23 G37 G111 G117* G110 G115			*G23 G37 G111 G113 G117* *G118* G53 G112 G115			

Unique identities of male bears are in regular font and italicized for females.

Table 6.2: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for categorical habitat models describing the probability of occurrence for grizzly bear resting sites by land designation in west-central Alberta, Canada. Estimates for which the [CI] did not overlap zero are given in bold.

		Reclaimed mine				**Protected area**				**Crown land**			
Variable		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
Habitat class													
	Barren	**−2.794**	**1.054**	**−4.862**	**−0.727**	**−34.792**	**1.254**	**−37.250**	**−32.334**	**−15.837**	**0.601**	**−17.015**	**−14.660**
	Herbaceous	−0.687	0.647	−1.956	0.582	**−18.195**	**1.029**	**−20.213**	**−16.178**	**−1.720**	**0.679**	**−3.051**	**−0.390**
	Shrub	−2.082	1.738	−5.489	1.325	−1.845	1.141	−4.083	0.392	**−1.369**	**0.467**	**−2.285**	**−0.454**
	Mixed forest	−0.343	1.263	−2.818	2.132	−0.461	1.336	−3.080	2.157	−0.511	0.448	−1.389	0.367
	Open conifer	**15.717**	**0.964**	**13.829**	**17.606**	−1.889	1.609	−5.043	1.264	**−1.332**	**0.528**	**−2.368**	**−0.296**
	Moderate conifer	−1.389	1.221	−3.783	1.005	−0.341	0.794	−1.897	1.216	−0.310	0.291	−0.880	0.260
Constant													
Model eval.		χ^2	df	P		χ^2	df	P		χ^2	df	P	
	Wald test	535.7	6	<0.0001		1516.8	6	<0.0001		905.8	6	<0.0001	
	ROC (AUC)	0.73				0.87				0.68			
	Cut-off probab.	0.5				0.5				0.5			

Dense conifer was withheld as a reference category

Table 6.3: Model structure and deviance for top 3 resting-site selection models (RSFs) for grizzly bear resting on reclaimed mines in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. The top resting-site selection models were selected from candidate food, security and combined food and security models also selected via Δ_i and w_i. Only the top models from the latter categories are given below with the full set of models available in the Table S.2 (Supplementary material). The best overall model is given in bold.

	Model	**K_i**	**-2LL**	**% Dev. explained**	**AIC$_c$**	**Δ_i**	**w_i**
	Null model	1	72.1	0.0	74.2	12.5	0.00
Forage							
	Richness + Berries + SSI	4	64.4	10.7	73.5	11.8	0.00
	Berries + SSI	3	67.3	6.6	74.0	12.3	0.00
Security							
	V cover + H cover + Dist trail + Dist trail^2 + Dist edge + Dist edge^2 + SSI	**8**	**41.2**	**42.9**	**61.7**	**0.0**	**0.49**
	V cover + H cover + Dist edge + Dist edge^2 + SSI	6	49.3	31.7	63.7	2.0	0.18
	Dist edge + Dist edge^2 + SSI	4	56.2	22.0	65.3	3.6	0.08
Forage & Security							
	Richness + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	46.8	35.0	64.2	2.5	0.14
	Berries + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	49.2	31.7	66.6	4.9	0.04
	Ungulate + Dist edge + Dist edge^2 + SSI	5	55.3	23.3	67.0	5.3	0.03
	Richness + Ungulate + Dist edge + Dist edge^2 + SSI	6	52.6	27.0	67.1	5.4	0.03

LL - log likelihood

% Dev. explained - percentage deviance explained

Table 6.4: Model structure and deviance for top 3 resting-site selection models (RSFs) for grizzly bear resting in protected areas in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. The top resting-site selection models were selected from candidate food, security and combined food and security models also selected via Δ_i and w_i. Only the top models from the latter categories are given below with the full set of models available in Table S.3 (Supplementary material). The best overall model is given in bold.

	Model	K_i	**-2LL**	**% Dev. explained**	**AIC$_c$**	Δ_i	w_i
	Null model	1	54.1	0.0	56.2	13.9	0.0
Forage							
	Berries + SSI	3	48.5	10.3	55.2	12.9	0.00
	Berries + Ungulate + SSI	4	46.6	13.8	55.7	13.5	0.00
Security							
	V cover + SSI	3	35.8	33.8	42.5	0.2	0.33
	V cover + H cover + SSI	4	35.1	35.2	44.2	1.9	0.14
	V cover + H cover + Dist trail + Dist trail^2 + Dist edge + Dist edge^2 + SSI	8	26.2	51.5	46.7	4.5	0.04
Forage & Security							
	Berries + V cover + H cover + SSI	**5**	**30.5**	**43.5**	**42.3**	**0.0**	**0.37**
	Berries + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	28.0	48.2	45.4	3.2	0.08
	Richness + V cover + H cover + SSI	5	34.8	35.6	46.5	4.3	0.04

LL - log likelihood

% Dev. explained - percentage deviance explained

Table 6.5: Model structure and deviance for top 3 resting-site selection models (RSFs) for grizzly bear resting on non-mined Crown (public) land in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. The top resting-site selection models were selected from candidate food, security and combined food and security models also selected via Δ_i and w_i. Only the top models from the latter categories are given below with the full set of models available in Table S.4 (Supplementary material). The best overall model is given in bold.

	Model	K_i	**-2LL**	**% Dev. explained**	**AIC$_c$**	Δ_i	w_i
	Null model	1	260.6	0.0	262.7	34.5	0.00
Forage							
	Richness + Berries + SSI	4	247.8	4.9	256.9	28.7	0.00
	Richness + Berries + Roots + Ungulate + SSI	6	243.2	6.7	257.7	29.5	0.00
	Richness + Ungulate + SSI	4	249.8	4.1	258.9	30.7	0.00
Security							
	V cover + H cover + Dist edge + Dist edge^2 + SSI	6	214.4	17.7	228.9	0.7	0.28
	V cover + H cover + Dist edge + Dist edge^2 + Slope + Slope^2 + SSI	8	209.6	19.6	230.1	1.8	0.16
	V cover + H cover + Dist trail + Dist trail^2 + Dist edge + Dist edge^2 + SSI	8	211.5	18.8	232.0	3.8	0.06
Forage & Security							
	Richness + V cover + H cover + Dist edge + Dist edge^2 + SSI	**7**	**210.8**	**19.1**	**228.2**	**0.0**	**0.40**
	Berries + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	214.4	17.7	231.8	3.6	0.07
	Richness + V cover + H cover + SSI	5	221.4	15.0	233.1	4.9	0.03

LL - log likelihood

% Dev. explained - percentage deviance explained

Table 6.6: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for top models describing the probability of occurrence for grizzly bear resting sites by land designation in west-central Alberta, Canada as assessed by Δ_i and w_i. Missing estimates for habitat features refer to variables not present in the respective model. Estimates for which the [CI] did not overlap zero are given in bold.

Variable	**Reclaimed mine**				**Protected area**				**Crown land**			
	β_i	Robust SE	95% CI		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
Forage												
Richness									0.659	0.373	−0.071	1.389
Berries					2.512	2.005	−1.418	6.441				
Security												
V cover	−0.163	0.104	−0.037	0.004	**0.046**	**0.014**	**0.019**	**0.074**	**0.025**	**0.006**	**0.014**	**0.036**
H cover	**0.869**	**0.329**	**0.224**	**1.514**	0.166	0.182	−0.190	0.522	**0.208**	**0.102**	**0.008**	**0.409**
Slope												
Slope^2												
Dist edge	−0.022	0.016	−0.054	0.010					**−0.019**	**0.006**	**−0.032**	**−0.007**
Dist edge^2	−0.022^	0.081^	−0.181^	0.137^					**0.065^**	**0.022^**	**0.023^**	**0.108^**
Dist trail	**0.103**	**0.004**	**0.002**	**0.019**								
Dist trail^2	−0.003^	0.006^	−0.181^	0.137^								
Comfort												
SSI	0.859	1.062	−1.223	2.941	1.649	0.922	−0.158	3.457	0.028	0.485	−0.923	0.979
Model eval.	χ^2	df	P		χ^2	df	P		χ^2	df	P	
Wald test	20.5	7	0.005		14.6	4	0.006		37.9	6	<0.0001	
ROC (AUC)	0.91				0.90				0.78			
Cut-off probab.	0.508				0.501				0.500			

^ Coefficient reported at 10^3 times its actual value

Table 6.7: Model structure and deviance for top GLM models testing the influence of season, land designation and time of day on selection ratios for grizzly bear resting in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i.

Model	K_i	**-2LL**	**% Dev. explained**	**AIC$_c$**	Δ_i	w_i
V cover selection ratio						
Null model	1	1351.9	0.0	1354.0	23.1	0.00
Land designation + Season + Land designation × Season	4	1321.9	10.2	1331.0	0.0	1.00
H cover selection ratio						
Null model	1	627.8	0.0	629.9	15.3	0.00
Land designation + Season + Land designation × Season	4	605.6	7.7	614.7	0.0	0.99
Dist to edge selection ratio						
Null model	1	1088.9	0.0	1091.0	22.2	0.00
Land designation + Time of day + Land designation × Time of day	4	1059.7	9.9	1068.8	0.0	0.49
Dist to trail selection ratio						
Null model	1	992.3	0.0	994.4	0.3	0.19
Land designation	2	989.8	0.9	994.1	0.0	0.22

All dependent variables were log-transformed to create a Gaussian distribution

LL - log likelihood

% Dev. explained - percentage deviance explained

Table 6.8: Estimated coefficients (β_i), robust standard errors [SE] and 95% confidence intervals [CI] for top models describing log selection ratios for vertical (V) and horizontal (H) cover at grizzly bear resting sites in west-central Alberta, Canada as assessed by Δ_i and w_i. Missing estimates for habitat features refer to variables not present in the respective model. Estimates for which the confidence intervals do not overlap 0 are given in bold.

		V cover				H cover			
Variable		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
Land design.									
	Protected	1.806	1.564	−1.259	4.871	−0.154	0.327	−0.794	0.487
	Crown	−1.372	1.333	−3.984	1.239	−0.524	0.276	−1.065	0.016
Season									
	Summer	−1.887	1.432	−4.693	0.919	**−0.721**	**0.274**	**−1.258**	**−0.183**
	Fall	2.583	1.720	−0.788	5.954	0.391	0.301	−0.199	0.981
Time of day									
	Nocturnal								
Interactions									
	Summer × Protected	0.815	2.257	−3.609	5.239	**1.057**	**0.492**	**0.093**	**2.021**
	Summer × Crown	1.763	1.492	−1.161	4.686	**0.768**	**0.306**	**0.169**	**1.367**
	Fall × Protected	**−5.098**	**2.002**	**−9.021**	**−1.175**	−0.746	0.403	−1.536	0.044
	Fall × Crown	−2.497	1.769	−5.963	0.970	−0.456	0.333	−1.110	0.198
Constant		2.094	1.291	−0.435	4.624	0.750	0.251	0.257	1.242

The following strata within variables were withheld as reference category:

Reclaimed mine (Land designation); Spring (Season); Diurnal (Time of day)

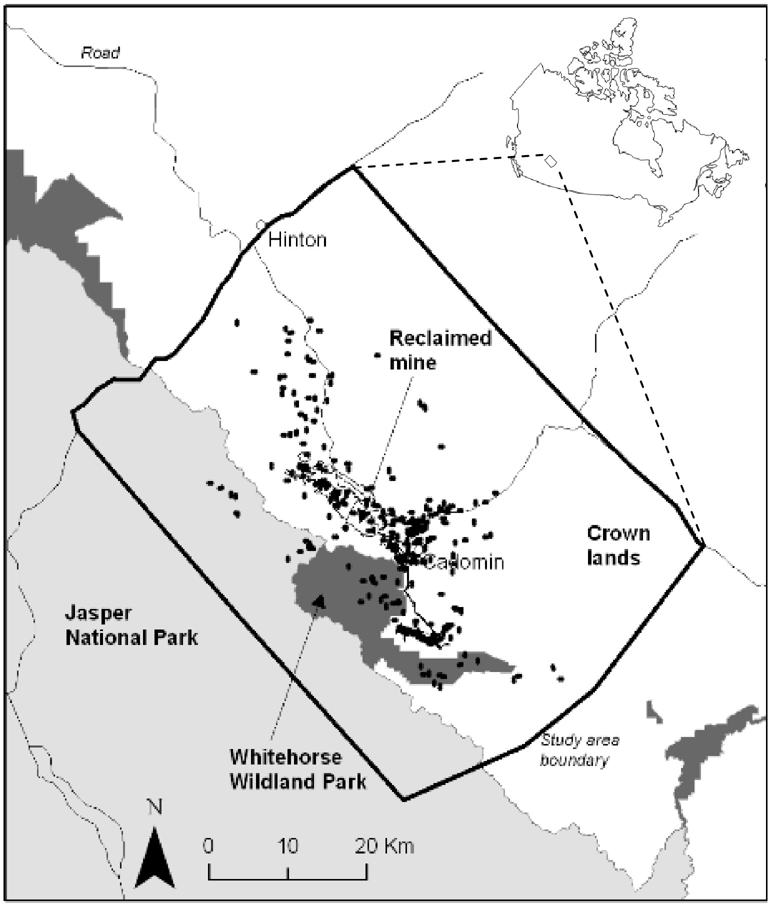

Figure 6.1: Study area for grizzly bear resting behaviour in relation to perceived human-derived risk in west-central Alberta, Canada, including major roads and colour coded land designations: reclaimed mines and Crown lands (white), protected areas (National park, dark gray; Wildland Park, light gray). Black dots are grizzly bear bedding (n_1 = 279) and paired random (n_2 = 279) sites 300 m away from bedding sites, visited in the field in 2009 and 2010.

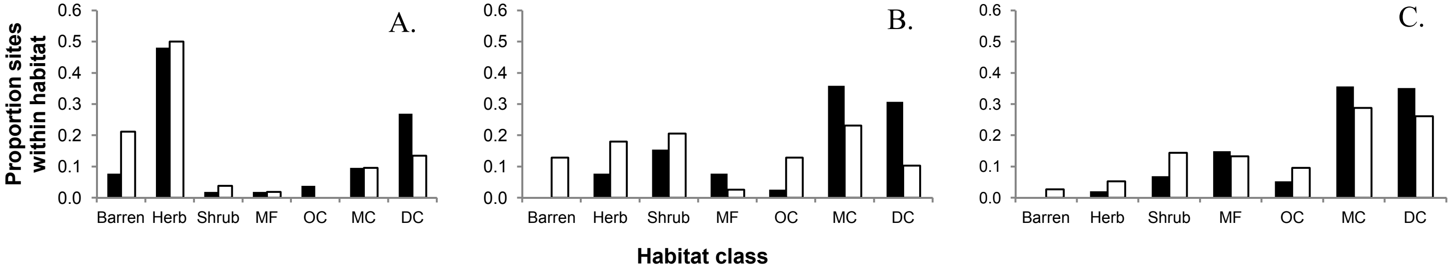

Figure 6.2: Habitat class at 279 grizzly bear resting sites and 279 random sites in west-central Alberta, Canada, by land designation: A. Reclaimed mines (*n_1* = 52 bedding sites), B. protected areas (*n_2* = 39 bedding sites) and C. Crown lands (*n_3* =188 bedding sites). Classification includes barren land (Barren), herbaceous (Herb), shrub (Shrub), mixed forest (MF), open conifer forest (OC), moderate conifer forest (MC) and dense conifer forest (DC).

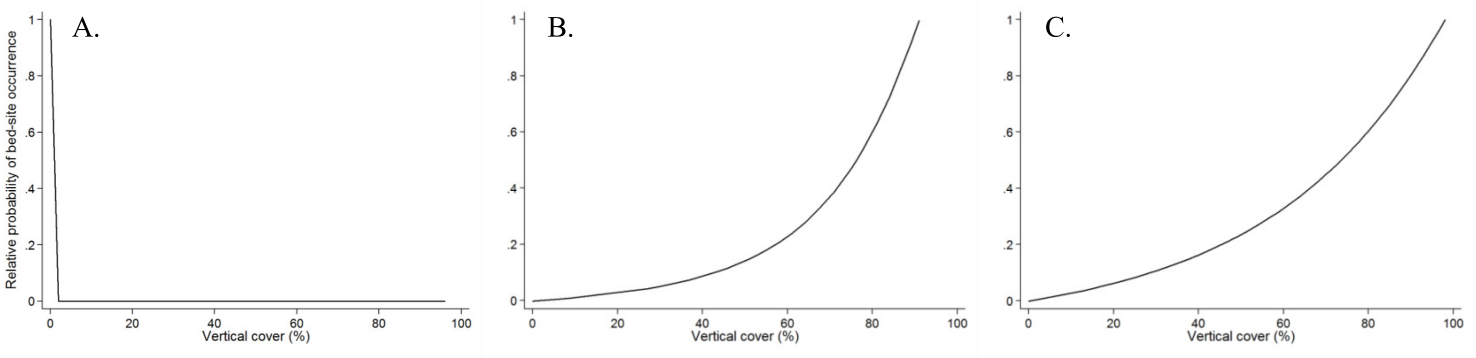

Figure 6.3: Relative probability of occurrence from AIC$_c$-selected grizzly bear resting-site selection models on reclaimed mines (A), protected areas (B), and Crown lands (C) in west-central Alberta, Canada, given vertical cover.

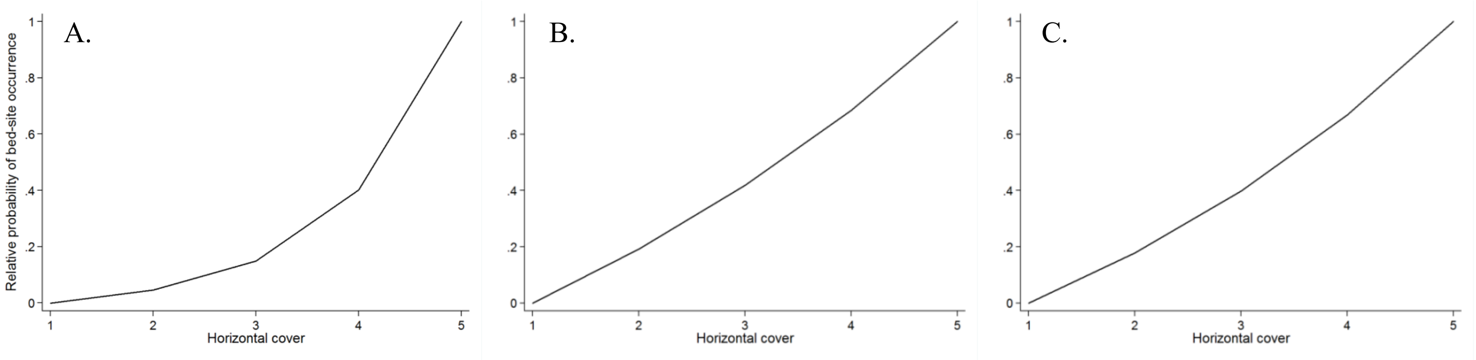

Figure 6.4: Relative probability of occurrence from AIC$_c$-selected grizzly bear resting-site selection models on reclaimed mines (A), protected areas (B), and Crown lands (C) in west-central Alberta, Canada, given horizontal cover.

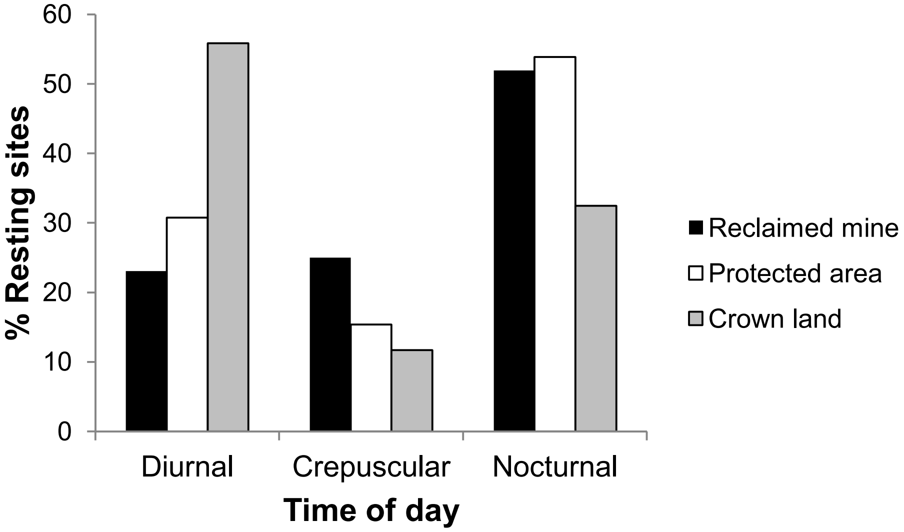

Figure 6.5: Onset time of grizzly bear resting in west-central Alberta, Canada by land designation: reclaimed mines (n_1 = 52 bedding sites), protected areas (n_2 = 39 bedding sites) and Crown lands (n_3 =188 bedding sites). Time of bedding includes diurnal (sunrise to sunset), crepuscular (morning twilight to sunrise and sunset to evening twilight) and nocturnal (evening twilight to morning twilight).

SUPPLEMENTARY MATERIAL

Table S.1: Model structure, deviance, significance and goodness-of-fit (Wald χ^2) for top GLM models testing the influence of season, land designation and time of day on vertical and horizontal cover selection ratios for grizzly bear resting in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. The full set of candidate models including the null models is provided below.

Model	K_i	**-2LL**	**% Dev. explained**	**AIC$_c$**	Δ_i	w_i
V cover selection ratio						
Null model	1	1351.9	0.0	1354.0	23.1	0.00
Season	2	1347.6	1.5	1351.9	21.0	0.00
Land designation	2	1343.3	3.0	1347.6	16.6	0.00
Time of day	2	1349.5	0.9	1253.8	22.8	0.00
Season + Land designation	3	1339.9	4.2	1346.5	15.6	0.00
Season + Time of day	3	1345.1	2.4	1351.8	20.8	0.00
Land designation + Time of day	3	1342.1	3.5	1348.7	17.8	0.00
Season + Land designation + Time of day	4	1338.6	4.6	1347.8	16.8	0.00
Land designation + Season + Land designation × Season	4	1321.9	10.2	1331.0	0.0	1.00
Season + Time of day + Season × Time of day	4	1342.6	3.3	1351.7	20.7	0.00
Land designation + Time of day + Land designation × Time of day	4	1335.4	5.8	1344.5	13.5	0.00
H cover selection ratio						
Null model	1	627.8	0.0	629.9	15.3	0.00
Season	2	626.1	0.6	630.4	15.8	0.00
Land designation	2	625.9	0.6	630.2	15.5	0.00
Time of day	2	627.7	0.0	632.0	17.4	0.00
Season + Land designation	3	624.1	1.3	630.7	16.1	0.00
Season + Time of day	3	626.1	0.6	632.7	18.1	0.00
Land designation + Time of day	3	625.5	0.8	632.1	17.5	0.00
Season + Land designation + Time of day	4	623.9	1.4	633.0	18.3	0.00
Land designation + Season + Land designation*Season	4	605.6	7.7	614.7	0.0	0.99
Season + Time of day + Season × Time of day	4	615.7	4.3	624.8	10.2	0.01
Land designation + Time of day + Land designation × Time of day	4	622.7	1.8	631.9	17.2	0.00

Table S.2: Model structure and deviance for candidate models for grizzly bear resting on reclaimed mines in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. The top resting-site selection models were selected from candidate food, security and combined food and security models also selected via Δ_i and w_i.

	Model	K_i	**-2LL**	**% Dev. explained**	**AIC$_c$**	Δ_i	w_i
	Null model	1	72.1	0.0	74.2	3.0	0.08
Forage							
	Richness + SSI	3	64.6	10.4	71.2	0.0	0.35
	Berries + SSI	3	67.1	6.9	73.8	2.6	0.10
	Roots + SSI	3	69.4	3.7	76.1	4.9	0.03
	Ungulate + SSI	3	69.0	4.3	75.6	4.4	0.04
	Richness + Berries + SSI	4	64.2	11.0	73.3	2.1	0.13
	Richness + Roots + SSI	4	64.4	10.7	73.5	2.3	0.11
	Richness + Ungulate + SSI	4	64.4	10.7	73.5	2.3	0.11
	Berries + Ungulate + SSI	4	66.6	7.7	75.7	4.5	0.04
	Richness + Berries + Roots + Ungulate + SSI	6	63.8	11.4	78.3	7.1	0.01
Security							
	V cover + SSI	3	67.5	6.4	74.1	12.6	0.00
	H cover + SSI	3	63.9	11.3	70.5	9.0	0.01
	V cover + H cover + SSI	4	63.9	11.3	73.0	11.5	0.00
	Dist edge + Dist edge^2 + SSI	4	56.1	22.2	65.2	3.6	0.10
	V cover + H cover + Dist edge + Dist edge^2 + SSI	6	49.1	31.9	63.6	2.1	0.21
	V cover + H cover + Dist edge + Dist edge^2 + Slope + Slope^2 + SSI	8	47.2	34.5	67.7	6.1	0.03
	Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	6	68.8	4.6	83.3	21.7	0.00
	V cover + H cover + Dist road + Dist road^2 + Dist trail + Distr trail^2 + SSI	8	62.2	13.7	82.7	21.2	0.00
	V cover + H cover + Dist road + Dist road^2 + Slope + Slope^2 + SSI	8	56.7	21.4	77.2	15.6	0.00
	V cover + H cover + Dist road + Dist road^2 + Dist edge + Dist edge^2 + SSI	8	45.6	36.7	66.1	4.6	0.06
	V cover + H cover + Dist trail + Dist trail^2 + Slope + Slope^2 + SSI	8	55.0	23.7	75.5	13.9	0.00
	V cover + H cover + Dist trail + Dist trail^2 + Dist edge + Dist edge^2 + SSI	8	41.0	43.1	61.5	0.0	0.59
	Elevation + Slope + Slope^2 + SSI	5	60.2	16.5	71.9	10.4	0.00
	V cover + H cover + Elevation + Slope + Slope^2 + SSI	7	56.5	21.6	73.9	12.4	0.00
Forage & Security							
	Richness + V cover + H cover + SSI	5	60.7	15.8	72.4	8.1	0.01
	Richness + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	47.0	34.9	64.4	0.0	0.53
	Richness + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	7	62.4	13.4	79.8	15.5	0.00
	Berries + V cover + H cover + SSI	5	63.0	12.5	74.8	10.4	0.00
	Berries + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	49.1	31.9	66.5	2.2	0.18
	Roots + V cover + H cover + SSI	5	63.1	12.4	74.9	10.5	0.00

Table S.2 Continued

Model	K_i	-2LL	% Dev. explained	AIC$_c$	Δ_i	w_i
Roots + V cover + H cover + Slope + Slope^2 + SSI	7	55.3	23.3	72.7	8.3	0.01
Ungulate + Dist edge + Dist edge^2 + SSI	5	55.2	23.5	66.9	2.5	0.15
Ungulate + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	7	68.2	5.4	85.6	21.3	0.00
Ungulate + V cover + H cover + Slope + Slope^2 + SSI	7	56.2	22.1	73.6	9.2	0.01
Richness + Ungulate + Dist edge + Dist edge^2 + SSI	6	53.1	26.4	67.5	3.2	0.11
Richness + Ungulate + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	8	62.1	13.8	82.6	18.3	0.00
Richness + Berries + Roots + Ungulate + V cover + H cover + SSI	8	59.7	17.2	80.2	15.8	0.00

% Dev. explained - percentage deviance explained

Table S.3: Model structure and deviance for candidate models for grizzly bear resting in protected areas in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. The top bedding site selection models were selected from candidate food, security and combined food and security models also selected via Δ_i and w_i.

	Model	K_i	**-2LL**	**% Dev. explained**	**AIC$_c$**	Δ_i	w_i
	Null model	1	54.1	0.0	56.2	1.0	0.15
Forage							
	Richness + SSI	3	52.4	3.0	59.1	3.9	0.04
	Berries + SSI	3	48.5	10.2	55.2	0.0	0.25
	Roots + SSI	3	53.0	2.0	59.6	4.4	0.03
	Ungulate + SSI	3	51.2	5.4	57.8	2.6	0.07
	Richness + Berries + SSI	4	47.1	12.9	56.2	1.0	0.15
	Richness + Roots + SSI	4	51.5	4.7	60.7	5.5	0.02
	Richness + Ungulate + SSI	4	50.6	6.4	59.7	4.5	0.03
	Berries + Ungulate + SSI	4	46.6	13.8	55.7	0.5	0.19
	Richness + Berries + Roots + Ungulate + SSI	6	42.6	21.1	57.1	1.9	0.09
Security							
	V cover + SSI	3	35.8	33.7	42.5	0.0	0.57
	H cover + SSI	3	45.9	15.1	52.5	10.1	0.00
	V cover + H cover + SSI	4	35.1	35.1	44.2	1.7	0.24
	Dist edge + Dist edge^2 + SSI	4	51.0	5.7	60.1	17.6	0.00
	V cover + H cover + Dist edge + Dist edge^2 + SSI	6	33.5	38.0	48.0	5.5	0.04
	V cover + H cover + Dist edge + Dist edge^2 + Slope + Slope^2 + SSI	8	33.5	38.1	54.0	11.5	0.00
	Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	6	50.0	7.5	64.5	22.0	0.00
	V cover + H cover + Dist road + Dist road^2 + Dist trail + Distr trail^2 + SSI	8	27.8	48.6	48.3	5.8	0.03
	V cover + H cover + Dist road + Dist road^2 + Slope + Slope^2 + SSI	8	34.8	35.6	55.3	12.9	0.00
	V cover + H cover + Dist road + Dist road^2 + Dist edge + Dist edge^2 + SSI	8	33.1	38.8	53.6	11.1	0.00
	V cover + H cover + Dist trail + Dist trail^2 + Slope + Slope^2 + SSI	8	27.7	48.7	48.2	5.8	0.03
	V cover + H cover + Dist trail + Dist trail^2 + Dist edge + Dist edge^2 + SSI	8	26.2	51.5	46.7	4.3	0.07
	Elevation + Slope + Slope^2 + SSI	5	53.0	2.0	64.7	22.2	0.00
	V cover + H cover + Elevation + Slope + Slope^2 + SSI	7	34.8	35.6	52.2	9.8	0.00
Forage & Security							
	Richness + V cover + H cover + SSI	5	33.2	38.6	44.9	2.6	0.15
	Richness + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	32.6	39.7	50.0	7.7	0.01
	Richness + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	7	49.3	8.8	66.7	24.5	0.00
	Berries + V cover + H cover + SSI	5	30.5	43.5	42.3	0.0	0.58
	Berries + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	28.0	48.1	45.4	3.2	0.12
	Roots + V cover + H cover + SSI	5	35.0	35.3	46.7	4.5	0.06

Table S.3 Continued

Model	K_i	-2LL	% Dev. explained	AIC$_c$	Δ_i	w_i
Roots + V cover + H cover + Slope + Slope^2 + SSI	7	34.7	35.7	52.1	9.9	0.00
Ungulate + Dist edge + Dist edge^2 + SSI	5	49.3	8.7	61.1	18.8	0.00
Ungulate + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	7	47.1	12.9	64.5	22.2	0.00
Ungulate + V cover + H cover + Slope + Slope^2 + SSI	7	34.6	36.1	52.0	9.7	0.00
Richness + Ungulate + Dist edge + Dist edge^2 + SSI	6	49.0	9.4	63.5	21.2	0.00
Richness + Ungulate + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	8	46.7	13.7	67.2	24.9	0.00
Richness + Berries + Roots + Ungulate + V cover + H cover + SSI	8	26.1	51.7	46.6	4.4	0.07

% Dev. explained - percentage deviance explained

Table S.4: Model structure and deviance for candidate models for grizzly bear resting on non-mined Crown (public) land in west-central Alberta, Canada. Model assessment was done by ranking AIC$_c$ values (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. The top bedding site selection models were selected from candidate food, security and combined food and security models also selected via Δ_i and w_i.

	Model	**K_i**	**-2LL**	**% Dev. explained**	**AIC$_c$**	**Δ_i**	**w_i**
	Null model	1	260.6	0.0	262.7	2.3	0.06
Forage							
	Richness + SSI	3	255.3	2.0	262.0	1.6	0.09
	Berries + SSI	3	255.7	1.9	262.3	1.9	0.08
	Roots + SSI	3	259.8	0.3	266.4	6.0	0.01
	Ungulate + SSI	3	256.5	1.6	263.1	2.7	0.05
	Richness + Berries + SSI	4	251.3	3.6	260.4	0.0	0.20
	Richness + Roots + SSI	4	254.8	2.2	263.9	3.5	0.04
	Richness + Ungulate + SSI	4	251.7	3.4	260.8	0.4	0.16
	Berries + Ungulate + SSI	4	251.5	3.5	260.7	0.2	0.18
	Richness + Berries + Roots + Ungulate + SSI	6	246.8	5.3	261.2	0.8	0.13
Security							
	V cover + SSI	3	237.9	8.7	244.5	15.7	0.00
	H cover + SSI	3	244.4	6.2	251.0	22.2	0.00
	V cover + H cover + SSI	4	226.9	12.9	236.0	7.2	0.01
	Dist edge + Dist edge^2 + SSI	4	249.3	4.3	258.4	29.6	0.00
	V cover + H cover + Dist edge + Dist edge^2 + SSI	6	214.3	17.8	228.8	0.0	0.52
	V cover + H cover + Dist edge + Dist edge^2 + Slope + Slope^2 + SSI	8	209.5	19.6	230.0	1.2	0.28
	Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	6	253.4	2.8	267.9	39.1	0.00
	V cover + H cover + Dist road + Dist road^2 + Dist trail + Distr trail^2 + SSI	8	221.9	14.8	242.4	13.6	0.00
	V cover + H cover + Dist road + Dist road^2 + Slope + Slope^2 + SSI	8	223.5	14.2	244.0	15.2	0.00
	V cover + H cover + Dist road + Dist road^2 + Dist edge + Dist edge^2 + SSI	8	212.1	18.6	232.6	3.8	0.08
	V cover + H cover + Dist trail + Dist trail^2 + Slope + Slope^2 + SSI	8	223.4	14.3	243.9	15.1	0.00
	V cover + H cover + Dist trail + Dist trail^2 + Dist edge + Dist edge^2 + SSI	8	211.4	18.9	231.9	3.1	0.11
	Elevation + Slope + Slope^2 + SSI	5	255.8	1.8	267.5	28.7	0.00
	V cover + H cover + Elevation + Slope + Slope^2 + SSI	7	224.5	13.9	241.9	13.1	0.00
Forage & Security							
	Richness + V cover + H cover + SSI	5	221.4	15.1	233.1	4.0	0.09
	Richness + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	211.7	18.8	229.1	0.0	0.67
	Richness + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	7	248.4	4.7	265.8	36.7	0.00
	Berries + V cover + H cover + SSI	5	226.8	13.0	238.6	9.4	0.01
	Berries + V cover + H cover + Dist edge + Dist edge^2 + SSI	7	214.3	17.8	231.7	2.6	0.19
	Roots + V cover + H cover + SSI	5	225.2	13.6	236.9	7.8	0.01

Table S.4 Continued

Model	K_i	-2LL	% Dev. explained	AIC$_c$	Δ_i	w_i
Roots + V cover + H cover + Slope + Slope^2 + SSI	7	223.9	14.1	241.3	12.2	0.00
Ungulate + Dist edge + Dist edge^2 + SSI	5	246.0	5.6	257.7	28.6	0.00
Ungulate + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	7	248.1	4.8	265.5	36.4	0.00
Ungulate + V cover + H cover + Slope + Slope^2 + SSI	7	221.7	14.9	239.1	9.9	0.00
Richness + Ungulate + Dist edge + Dist edge^2 + SSI	6	243.7	6.5	258.2	29.0	0.00
Richness + Ungulate + Dist road + Dist road^2 + Dist trail + Dist trail^2 + SSI	8	243.8	6.5	264.3	35.1	0.00
Richness + Berries + Roots + Ungulate + V cover + H cover + SSI	8	215.7	17.2	236.2	7.0	0.02

% Dev. explained - percentage deviance explained

CHAPTER 7

DISSERTATION SUMMARY

Ecosystems are experiencing extinction of component species at rates unprecedented in historical time. Most of Earth's biological systems have been affected by man whether directly or indirectly. Given the conservation challenges affecting taxa across a diversity of ecosystems, it is paramount that ecologists focus on addressing research questions with conservation relevance. Addressing applied ecological questions can still involve testing of ecological theory. Incorporating conservation related topics routinely into research programs would allow ecologists to deliver science products that benefit the natural world and are representative of society's interests.

Habitat modification/loss is arguably the major contemporary challenge to species persistence and part of the extinction quartet singled out by Diamond (1984). Open-pit mining provides an extreme example of this issue. Human-caused disturbances such as an open-pit mine are different than most natural disturbances (e.g., fire), but might resemble landslide. While fire is a natural agent of change in many ecosystems facilitating succession and diversity, an open-pit mine or landslide strips soils, exposing rock and triggering mineral leeching. Following mine closure, vegetation composition on reclaimed mines is largely determined by reclamation practitioners. Planting vegetation that attracts herbivores can result in herbivore densities higher than in the original system, and could increase predator density. Context, deciding on target species, and choice of indicators are essential in defining what constitutes reclamation success.

Reclamation versus restoration are different concepts (Bradshaw 1996) and certainly reclaimed mines have lower biodiversity than the area before mining. We can hope that presence of herbivores and predators on a disturbed landscape can, through plant dispersal, defecation, and animal and plant death, promote nutrient cycling and in the long-term result in a self-sustaining system that resembles the original state. However, visible effects may not be noticeable in a researcher's lifetime, and current mine reclamation practice often does not have the target of recreating the community that was present before mining. Some species, for example certain large carnivores, may take a long time to colonize disturbed sites, and their populations might be directly affected through mortality at the active mining stage (e.g., road collisions) or following reclamation (e.g., illegal shooting in the absence of regulated human access). In addition, mining may potentially have indirect effects on fitness of facultative and/or obligate carnivore if it decreases food availability, reduces secure habitat for resting, or results in barriers to movement.

The effects of human activity on wildlife behaviour can be paralleled with prey response to predation risk (Frid and Dill 2002). For large mammalian carnivores, humans can be viewed as analogue to 'predators', a reality eloquently exemplified by widespread persecution of predators in North America including in much of the twentieth century. Despite extensive historical efforts to limit or even eradicate carnivores, our fascination with these animals is deeply rooted, perhaps stemming from immemorial times, when our ancestors competed with carnivores for survival. Today, we are outcompeting them by orders of magnitude, as illustrated by well-documented range declines of carnivores.

Increasingly, attitudes of humans towards top predators are shifting from widespread eradication to recognition of the value of predators in the food web. Such shifts are more common for predators that are unlikely to cause bodily harm to people, or where predators do not threaten livelihoods. However, human-carnivore interactions and potential negative effects on carnivore survival might well increase given projections on human population growth and intensifying human activity in previously undisturbed areas inhabited by carnivores. Understanding the consequences of human activity such as habitat modification through industrial expansion, or human access (e.g., recreation) on carnivore behaviour can be used to inform strategies for environmental mitigation.

Documenting the effects of mining on carnivores is needed given that knowledge to date is sparse and comes primarily from studies on ungulates (e.g., MacCallum and Geist 1992, Merrill et al. 1994, Weir et al. 2007). Such knowledge is particularly needed for the province of Alberta because of the substantial extent of underground resources in the province (e.g., 70% of Canada's coal). Multiple coal leases are active or proposed in Alberta, with much of the coal seam concentrated at the interface of the foothills and eastern slopes of the Rocky Mountains. This area also is undergoing oil and gas development, logging and recreational activities, and the cumulative effects of these human activities on wildlife can be substantial (Schneider et al. 2003).

The grizzly bear (*Ursus arctos*) is a facultative carnivore/omnivore that has been studied for many years, with one of the classical studies conducted by the Craighead brothers in Yellowstone National Park (Craighead 1982, Craighead et al. 1995). Since then, long-term grizzly bear research projects have been ongoing in Canada and USA, with additional major projects on brown bears in Scandinavia, and a variety of shorter term projects scattered throughout the world. A search performed in Web of Science in December 2012, by topic 'grizzl* bear*', revealed 1,580 published papers, with an entire journal (*Ursus*) dedicated to bear research. While much is already known about this species, vast knowledge gaps exist, particularly in relation to bear behavioural response to industrial activities such as mining development, post-mining reclamation, and human recreation.

This thesis presents results of an investigation of bear space use in response to mining at different phases, while also comparing bear diet and resting-site selection on reclaimed mines, neighbouring protected mountainous areas, and unprotected public lands in the foothills. An important contribution is disentangling the relationship between bears and altered food sources on mined landscapes. In addition, the thesis advances methods for indentifying complex behaviour from GPS radiocollar technology, relates resting behaviour to human-derived risk perception, and tests key assumptions of caching in a facultative carnivore.

Contrary to expectations, I found that landscapes disturbed by open-pit mining at Luscar and Gregg River mines were used by grizzly bears after mine closure (2006 and 2008-2010), and also during active mining (1999-2003) (Chapter 2). All reproductive classes selected reclaimed and expecially undisturbed (treed) areas on mines, but active and inactive areas also were used. Females with cubs appeared most adaptable to mining operations, having the greatest home range overlap with mineral disturbance limits. Their shorter movements during mining suggest they cautiously navigate an active mining landscape, whereas their longer movements following reclamation may be indicative of unrestricted space use. Males had lower home range overlap than females during active mining, and their movements were longer suggesting an avoidance of human activity associated with mining. After mine closure, males had shorter movements indicate of foraging on legumes and graminoids planted as part of reclamation.

The multinomial modeling framework proposed in Chapter 3 had high power of prediction particularly for ungulate consumption by grizzly bears, distinguishing it from vegetation feeding or bedding. The ability to predict multiple behavioural states from GPS radiocollar datasets provides a biologically meaningful understanding of animal movement and is a timely achievement given the widespread use of GPS tracking technology. For grizzly bears in west-central Alberta this approach showed more ungulate consumption in the foothills compared to mountains or reclaimed mines, and the fact that bears do not typically consume vegetative foods at sites where they rest in the foothills.

Reclamation to wildlife habitat using legumes provides grazing material for grizzly bears and ungulates, with elk, deer and bighorn sheep more likely to be present on mines than neighbouring undisturbed areas (Chapter 4). Moose was the only ungulate more likely to occur outside mines, likely because shrub areas where moose forage have low extent on mines. Despite the availability of ungulates on reclaimed mines, predators including bears are detectable by ungulates on these open areas, which makes the ungulates difficult for the bears to capture. Bear diet reflected the availability of foods, with bears switching diet as a function of mining and elevation. Herbaceous material dominated diet on reclaimed mines, sweetvetch (*Hedysarum* spp.) roots dominated diet in the mountains, and ungulates represented the major food item in the foothills. Altough legumes (e.g., clover [*Trifolium* spp.], sweet-clover [*Melilotus* spp.], and alfalfa [*Medicago* spp.]) are consumed by bears and important for nitrogen fixation and slope stabilization, they are not native to Alberta and hence decrease biodiversity intactness (Nielsen et al. 2007).

Grizzly bears consumed ungulates in areas that provided cover, primarily moderate and dense conifer forest (Chapter 5). Because a larger proportion of meat in the diet is related to increased reproductive output in this species, facilitating meat consumption is important particularly in the context of threatened bear populations. The majority of ungulate consumption sites on reclaimed mines were located inside tree patches left undisturbed during active mining. These tree 'islands' are essential components for grizzly bears on mined landscapes and should be maintained during mining. In addition to providing meat consumption opportunities, they also serve as reservoirs for native plant species thus facilitating colonization of nearby grasslands by native species.

I found that although bears can be effective predators on neonate calves and fawns, they spent more time at large ungulate carcasses (Chapter 5), presumably because these provide high amounts of meat being highly valuable for bears. To minimize detection and thus meat loss to other predators, bears cached carcasses, with caching more likely for large prey. Caching behaviour is possible in forested areas but not on reclaimed mine grasslands because of poor soil and biological detritus, reinforcing the need for preserving treed areas during mining.

By analyzing resting (bedding)-site selection by bears, I showed that horizontal cover was important for resting on reclaimed mined, protected areas and Crown (public) lands (Chapter 6). Vertical cover also influenced selection of resting sites, with the exception of mines, where bears bedded in forested but also herbaceous areas. Resting sites were more likely to be far from designated access trails on mines, suggesting losses in habitat effectiveness (*sensu* Suring et al. [1998]) on reclaimed mines, potentially because bears perceive humans from far distances in relation to habitat openness. I also documented a temporal shift in timing of resting, with bears bedding more at night in protected areas and on reclaimed mines (both with low human access), but more during the day on Crown lands with high human activity, pointing to the importance of access management on this multiple-use landscape.

The openness of the area results in bears and other wildlife being easily visible and could potentially result in illegal shooting that could be prevented by rigorous law enforcement in the area. Another potential challenge associated with reclaimed mines is that concentrating bear foods in a confined area can risk attracting females with cubs and males as demonstrated in this thesis, possibly resulting in sexually selected infanticide. Monitoring cub survival and spatial interactions between males and females with cubs would be necessary to evaluate the effects of using artificial foods to concentrate grizzly bears of different reproductive classes on cannibalism and population age structure. Using mixtures of native plants to reflect vegetation communities present before mining would alleviate this issue, while also restoring biodiversity of the disturbed site.

A key direction for future work will be to continue researching bear behaviour on the mines once these sites have been reclaimed and are open to public access. Presence of humans on reclaimed mines might increase the risk of human-bear encounter because these areas are used by bears of all reproductive statuses for feeding. Opportunity exists for experimental manipulation on these sites, wherein certain trails could be opened to the public while others kept closed, and bear behaviour monitored at the minimum based on GPS radiocollar data. Camera traps could be set along trails to obtain types and levels of human access, because such information can be related to bear movement data and is useful for managing human access.

Similar to other investigations focused on wide-ranging, threatened mammalian species, sample sizes used in this study are sometimes relatively low, with primary analyses for some of the chapters involving as few as nine adult bears. Notwithstanding, I believe that my results are robust given the low density of bears in the study area (4.79 bears/1,000 km^2) (Boulanger et al. 2005), such that I studied a substantial proportion of the bear population.

While other North American carnivores such as black bears and cougars persist in close proximity to people, grizzly bear conservation is more challenging because of requirements for suitable seasonal foods, as well as perceived and real danger of conflict with people. Indeed, none of my study bears had its home range exclusively within mineral disturbance limits, implying that undisturbed wilderness areas (such as Whitehorse Wildland Park and Jasper National Park located nearby mines) might be required for bear persistence. However, my findings suggest that grizzly bears are adaptable to habitat change, even when change when takes an extreme form such as through open-pit mining. Beyond habitat modification and risks to bears associated with active industrial operations, the opening of areas to industrial development facilitates human access into previously remote regions. As identified in the Recovery Plan for grizzly bears in Alberta (Alberta Grizzly Bear Recovery Team 2008), long-term access management is essential to achieving population recovery. Without regulating human use of trails and roads, areas disturbed by industry that contain bear foods have the potential to become attractive sinks (*sensu* Delibes et al. 2001, Nielsen et al. 2006). For reclaimed mines in west-central Alberta, legumes and ungulates attract grizzly bears from neighbouring areas, but these sites could function as sinks if human-caused mortality risk associated with using mines is high.

LITERATURE CITED

Alberta Grizzly Bear Recovery Team. 2008. Alberta Grizzly Bear Recovery Plan 2008-2013. [online] URL: http://www.srd.alberta.ca/fishwildlife/wildlifeinalberta/grizzlybearmanagement/default.aspx

Boulanger, J., G. B. Stenhouse, M. Proctor, S. Himmer, D. Paetkau, and J. Cranston. 2005. 2004 Population inventory and density estimates for the Alberta 3B and 4B Grizzly bear management area. Report prepared for Alberta Sustainable Resource Development, Fish and Wildlife Division. Integrated Ecological Research, Nelson, BC, Canada.

Bradshaw, A. D. 1996. Underlying principles of restoration. Canadian Journal of Fisheries and Aquatic Sciences **53** (Suppl. 1):3-9.

Craighead, F. C. Jr. 1982. Track of the grizzly. Sierra Club Books, San Francisco.

Craighead, J. J., J. A. Mitchell, and J. S. Sumner. 1995. The grizzly bears of Yellowstone: Their ecology in the Yellowstone Ecosystem, 1959-1992. Island Press, Washington, DC, USA.

Delibes, M., P. Gaona, and P. Ferreras. 2001. Effects of an attractive sink leading into maladaptive habitat selection. American Naturalist **158**:277-285.

Diamond, J. M. 1984. Historic extinctions: A Rosetta Stone for understanding prehistoric extinctions. In eds. P. S. Martin, and R. G. Klein: Quaternary extinctions. University of Arizona Press, Tucson, AZ, USA.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**:11. [online] URL: http://www.consecol.org/vol6/iss1/art11

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology **77**:132-138.

MacCallum, B. N., and V. Geist. 1992. Mountain restoration: Soil and surface wildlife habitat. GeoJournal **27.1**:23-46.

Merrill, E. H., T. P. Hemker, K. P. Woodruff, and L. Kuck. 1994. Impacts of mining facilities on fall migration of mule deer. Wildlife Society Bulletin **22**:68-73.

Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation **130**:217-229.

Nielsen, S. E., E. M. Bayne, J. Schieck, J. Herbers, and S. Boutin. 2007. A new method to estimate species and biodiversity intactness using empirically derived reference conditions. Biological Conservation **137**:403-414.

Schneider, R. R., J. B. Stelfox, S. Boutin, and S. Wasel. 2003. Managing the cumulative impacts of land uses in the Western Canadian Sedimentary Basin: A modeling approach. Conservation Ecology **7**:8. [online] URL: http://www.consecol.org/vol7/iss1/art8

Suring, L. H., K. R. Barber, C. C. Schwartz, T. N. Bailey, W. C. Shuster, and M. D. Tetreau. 1998. Analysis of cumulative effects on brown bears on the Kenai Peninsula, southcentral Alaska. Ursus **10**:107-117.

Weir, J. N., S. P. Mahoney, B. McLaren, and S. H. Ferguson. 2007. Effects of mine development on woodland caribou *Rangifer tarandus* distribution. Wildlife Biology **13**:66-74.

APPENDIX 1

LAND-USE PLANNING FOLLOWING RESOURCE EXTRACTION – LESSONS FROM GRIZZLY BEARS AT RECLAIMED AND ACTIVE OPEN PIT MINES

ABSTRACT

Gauging the success of industrial reclamation requires targets to be set for restoring ecosystem structure and function. An indication of reclamation success is if wildlife recolonise, forage, rest, reproduce and survive on reclaimed areas. The grizzly bear is a threatened species that exists at low densities in Alberta, Canada and facilitates a variety of ecosystem processes. To make suggestions for mitigating the effects of open pit mining on this species, I collected and analysed biological data for grizzly bears on and around Cheviot, Luscar and Gregg River coal mines in west-central Alberta. During 2008–2010, I captured and attached GPS radio collars on 12 adult bears on and around mines which allowed me to intensively track their movements.

We visited bear-used GPS locations in the field to assess bear activity and microhabitat characteristics. Bears selected reclaimed mines and areas near mines extensively in late spring and early summer to forage on forbs sown as part of mine reclamation and to depredate ungulate calves and lambs. In the fall, bears moved primarily in areas outside mines to forage on berries in preparation for winter denning. Bears often bedded in dense tree cover which underlines the importance of maintaining original vegetation patches in planning mine operations. The animals sometimes crossed the major active mine haul road and moved on and near trails designated for human access on mine leases.

High mortality risk associated with expansion of human access into previously remote areas is a major threat to long-term persistence of the grizzly bear population. Defensive driving and potentially enforcement of speed restrictions on mine haul roads in areas with high frequency of bear crossings, provisioning for ecological movement corridors and proper waste management

practices will help prevent human-bear conflict during the active mining phase. Following closure of mines, access management along designated trails will reduce the risk of conflicts. Imposing access restrictions, along with preserving undisturbed habitat patches and restoring the original vegetation cover will enable coexistence of people and bears on a shared landscape.

INTRODUCTION

Open pit mining is a large-scale industrial activity that modifies habitat by reshaping landscapes and removing the original vegetation. Following closure of active mining operations the land is reclaimed with the reclamation objective being the progressive re-establishment of self-sustaining landscapes that incorporate wildlife habitat. Wildlife decolonisation of reclaimed areas is on its own not an appropriate indicator for the success of reclamation. Animals may perceive reclaimed areas to be unsuitable and simply move through without engaging in the full suite of natural behaviours. A more desirable measure of reclamation success is whether animals exhibit the full range of natural behaviours on reclaimed areas.

Current knowledge on the effects of active mining operations and reclamation on large mammals comes primarily from research on ungulates. Ungulate species may respond differently to surface mining activity and mine reclamation that carnivores. Caribou (*Rangifer tarandus*) can displace spatially up to 4 km away from active mine leases (Weir et al. 2007). Bighorn sheep (*Ovis canadensis*) appear to be less influenced by mining activity (Jansen et al. 2009) and readily recolonised and increased in abundance on Luscar and Gregg River reclaimed coal mines in west-central Alberta, from 35 pre-mining to currently around 1,000 individuals (BWT 2010). Elk (*Cervus elaphus*) numbers experienced a fast upward trend on the same reclaimed mines and currently number around 400 individuals (BWT 2010). The expansion was likely due to increased availability of forage for ungulates by sowing forbs, grasses and sedges as part of reclamation.

The effects of open pit mining on carnivores are largely unknown. Top carnivores are important in the structure and functioning of ecosystems and although their overall biomass is low compared to herbivores and plants, carnivores are crucial to maintaining biodiversity (Ale and Whelan 2008). The grizzly bear (*Ursus arctos horribilis*) is a keystone species iconic for the wilderness of the Rocky Mountains. Through deposition of scat, grizzly bears facilitate the dispersal and germination of plant seeds they consume (Willson and Gende 2004). When foraging by digging for plant roots, grizzly bears affect plant distributions and mineral nitrogen availability (Tardiff and Stanford 1998). Research in Alaska (Adams et al. 1995) and Yellowstone National Park (Mattson 1997) has showed that grizzly bears can have important effects on ungulate populations through predation.

Of all North American large carnivores, grizzly bears have low resiliency to human-born threats because of requirement for large patches of undisturbed habitat, low reproductive rates, and potential to get into conflict with humans (Weaver et al. 1996). Consequently, the grizzly bear has experienced dramatic decline throughout its range in North America (Servheen et al. 1999). Habitat fragmentation and persecution by humans are the major causes of the documented decline, which is well illustrated by the current status designation of the grizzly bear in Alberta, Canada (Threatened status conferred in 2010). The present range of grizzly bears in Alberta has been pushed westward by human encroachment and the majority of known grizzly bear mortalities are human-caused and occur within 500 m of a road or access trail (Benn and Herrero 2002).

The province-wide grizzly bear population estimate, based primarily on DNA sampling from bear hair collected at baited sites (Grizzly Bear Inventory Team 2007), showed that less than 800 grizzly bears occur outside National Parks, with the overall Alberta grizzly bear population being estimated at less than 1,000 individuals. A Grizzly Bear Recovery Plan for the province was put forward in 2008 (Alberta Grizzly Bear Recovery Team 2008). The Plan stresses that bear numbers are low because of human-caused mortalities associated with expansion of industry, recreation and agricultural practices. This has been supported by a recent review of grizzly bear status in the province (Government of Alberta 2010). The Plan underlines the need for studies that fill knowledge gaps on the effects of industrial developments on grizzly bear habitat, ecology and behaviour.

With resource extraction industries such as mining projected to expand in Alberta, an assessment is rapidly needed for the effects of mining on the grizzly bear. The purpose of this study was to assess grizzly bear response to open pit mining and reclamation, by documenting bear foraging, movement, habitat ecology and behaviour, on and around coal mine leases. As a case study, investigations focused on mineral surface leases (MSLs) located near the Hamlet of Cadomin, at the interface between the eastern slopes of the Rocky Mountains and foothills. Based on my research findings I also wanted to formulate suggestions for mine reclamation and active mining operations that minimised any negative effects of mining on grizzly bears.

METHODS

The field component of the study was carried out during 2008–2010 in west-central Alberta, at the interface between the eastern slopes of the Rocky Mountains and foothills. A 10,000 km^2 study area was delineated south of the town of Hinton, with the area being bordered to the north by Highway 16. The predominant natural land cover in the region is coniferous forest dominated by white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*) with deciduous forest composed of balsam polar (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*) also present at lower elevations and on sunny south and east facing slopes. Elevation and ruggedness are greater in the western section of the study area which is mountainous with the eastern section being characterised by rolling hills.

Human activities in the study area include: open-pit coal mining, forest harvesting, oil and gas development and recreational activities (All Terrain

Vehicles, hunting, hiking and camping) with the mountainous areas generally having less human activity. The area encompasses three open pit coal mine MSLs located near the Hamlet of Cadomin (population 60). Within a mining area, trees and other surface vegetation are removed and excavations are being done to extract coal. During this study, Luscar MSL had a total area of 4,381 ha, with 2,382 ha being disturbed, of which 1,195 ha were unreclaimed and 787 ha reclaimed. The 1,195 ha unreclaimed included 400 ha still supporting active mining. Gregg River had a total area of 3,700 ha of undisturbed and fully reclaimed lands. Cheviot MSL had an area of 1,600 ha of which 650 ha were active and 950 ha undisturbed. Other land designations in the study area include public (Crown) lands and protected areas (Whitehorse Wildland Park and part of the eastern sector of Jasper National Park) (Figure I.1).

Each year during spring and fall I captured and set GPS radio collars (Telus UHF; Followit, Sweden) on adult grizzly bears on and near the MSLs, with assistance from the Foothills Research Institute Grizzly Bear Program (Hinton, Alberta). All bears were captured and handled according to Animal Care and Use protocols approved by the University of Saskatchewan and University of Alberta. I used baited culvert traps, limited leg-hold snaring and remote darting from helicopter to capture bears and chemically immobilise them with a combination of Xylazine-Telazol (XZT) reversed by Atipamezole. Each radio collar had a unique radio beacon frequency allowing me to track individual bears in the field. I programmed the radio collars to acquire a GPS location every hour, 24 h/day, during March 15 to December 1 when the bears were mostly outside their winter dens. Based on field trials the GPS radio collar accuracy was ± 10 m.

Every month during the non denning period I located bears from the ground, fixed-wing aircraft or helicopter based on the collar VHF radio beacon. To acquire GPS locations from collared bears, I approached each bear to within a safe distance that allowed remote data downloads from the collars. I then downloaded the GPS collar data to a laptop computer and plotted the locations in a GIS system to visualise where the animal had moved during the past month. I selected a sample of locations for each bear during each month (largest four location clusters and random other clusters) and uploaded them to hand-held GPS units so that I could visit these sites in the field. During May–November, field crews hiked to visit the selected GPS locations where they recorded general habitat characteristics and bear activity. For safety and logistical reasons, visits occurred 2–4 weeks after the bear had left the general area.

We incorporated a temporal component in my data analysis to account for seasonal variation in grizzly bear food availability in my study area. Following Nielsen et al. (2004a), I divided my data into three seasons: “hypophagia” (spring; den emergence to June 14), “early hyperphagia” (summer; June 15 to August 7) and “late hyperphagia” (fall; August 8 to den entrance). Grizzly bears in west-central Alberta dig for sweet vetch roots (*Hedysarum* spp.) and feed on ungulate carcasses in hypophagia, graze forbs and grasses in early hyperphagia and feed on berries and ungulates in late hyperphagia (Munro et al. 2006).

Home Range Overlap with Mine Leases

Using 95% of the GPS locations acquired remotely from radio collared bears (to account for 5% potential GPS erroneous locations), I calculated fixed kernel bear home ranges for each of the three seasons. For each bear in each season, I extracted home range areas that overlapped MSLs and calculated the proportion of home range overlap with leases by dividing the home range area on a lease by the total home range area of the respective bear in a given season. Similarly, I calculated proportion of the home range area present outside leases and compared proportion of the home range that overlapped mines with the proportion that occurred outside mines.

Bear Activity on versus Outside Mines

We used data from visits of bear GPS location clusters sampled in the field to plot frequency of bear activity standardised to percentage. During the first month of 2008 field visits I investigated locations picked at random from the GPS radio collar data. Subsequently, because I was primarily interested in bear activity other than simple travel through an area, I focused visits on GPS location clusters where bears had spent at least three hours within a 30 m radius. Overall I recorded eight types of bear activity with some sites having more than one type of activity. Bear sign of activity that I recorded was either foraging (feeding on an ungulate carcass, ants or rodents, digging for plant roots, grazing on upper plant parts, or feeding on berries), resting (bedding) or possible territorial marking (claw marking on trees). For a small set of sites visited in the field (<4%) I was not able to identify bear activity despite intensive search efforts of the area.

Bedding and Ungulate Kill Site Selection

Because bedding and feeding on ungulate carcasses formed 80% of findings at GPS locations clusters visited in the field indicating that bears spend a lot of time engaged in these activities, I assessed the type of habitat these activities occurred in.

Because of small sample sizes for the Cheviot active MSL (13 sites), I performed the analyses for reclaimed mines only and classified habitat into three categories: forest (land cover undisturbed by mining i.e. original tree patches on MSLs), grassland (vegetated areas previously disturbed by surface mining and subsequently reclaimed to grasses and forbs) and barren land (unvegetated patches such as rocky formations and steep walls from old mine pits). I calculated Manly's habitat selection ratios for bear bedding and ungulate carcasses according to a use-availability design (Johnson et al. 2006). I sampled habitat availability by generating 238 (Gregg River MSL) and 400 (Luscar MSL) random GPS locations respectively with differences in number of random locations proportional to the difference in surface extents between Luscar and Gregg River MSLs. I focused on categorical habitat classes for this analysis because I was interested in assessing the extent to which these activities occur in undisturbed versus disturbed habitat on mines. Future analyses will incorporate other potentially important variables such as distance to habitat edges and ungulate availability on the landscape.

Cheviot Haul Road Crossings

The 23.84 km long Cheviot haul road follows for the most part the McLeod River Valley and receives traffic 24 h/day. The mean frequency of heavy haul truck traffic is one every 10 minutes, whereas light and support vehicles are intermittent. In order to investigate the possible impacts of active mine haul roads on grizzly bear movements and habitat use, I divided the Cheviot mine haul road into 500 m segments to calculate the frequency of road crossings by radio collared bears according to season. I connected 1-h consecutive GPS radio collar locations with straight lines and considered these as movement “steps” that the bears took on the landscape. I then intersected all steps that crossed the haul road with the 500 m road segments and mapped the frequency of road crossings. I recognise that this technique will represent a minimum number of crossings and is thus likely an underestimation of all crossings.

Bear Use of Areas near Mine Trails

Public access on MSLs is permitted only along designated access trails that are either non-motorised or motorised. To investigate bear use of areas near designated trails that cross reclaimed mines, I created 500 m buffers around each side of the trails. I considered motorised trails (ATV and dirt bike access permitted) separately from non-motorised trails (hiking, horseback riding and biking only allowed). I then counted the number of bear GPS locations within each buffer by season to identify trail type and season for which grizzly bear use of access trails and adjacent habitats is high.

We performed geospatial analyses in ArcMap v.9.2 (ESRI, Redlands, California), basic statistical calculations in Excel v.2007 (Microsoft, Redmond, Washington) and used STATA v.11.2 (StataCorp, College Station, Texas) to graph my results. Habitat selection ratios were computed using R (R Foundation for Statistical Computing, Vienna, Austria).

Data

In 2008–2010 I set radio collars on 12 adult bears (6 males; 6 females) in the study area which was assumed a random sample of the grizzly bear population of the area. One male slipped the collar off within a week of capture and a second male dropped the collar within a month. The ten remaining bears provided data for variable amounts of time, from one season to three years, depending on when the bear was captured, premature collar slip-off or collar malfunctioning (Table I.1). All ten bears crossed at least one of the three MSLs under study during the monitoring period.

RESULTS

Home Range Overlap with Mine Leases

Areas outside mine leases included higher proportions of bear home ranges than areas on mines (median >0.75). Of all mine leases considered, proportion home range overlap was highest for Luscar MSL, a pattern which was consistent regardless of season. Reclaimed mines (Luscar and Gregg River MSLs) made up the highest proportion of bear home ranges during early hyperphagia, when correspondingly areas outside mines had the lowest proportion of bear home ranges of all seasons. As expected, Cheviot MSL where active mining occurred had the lowest proportion of home range overlap. Individual variation between bears was apparent, with two bears (depicted as medium grey outliers in Figure I.2) having a large proportion of their home ranges on Gregg River MSL during hypophagia and early hyperphagia (median >0.4). In late hyperphagia, for most bears only a small proportion of home ranges overlapped reclaimed and active MSLs (median <0.05). Grizzly bears have large home range requirements because they need to cover vast areas in search for both food and mates. The MSLs considered in my study represented only a small proportion of where most bears moved during the monitoring period, but bears did use reclaimed mines for foraging, resting and tree marking (discussed below).

Bear Activity on versus Outside Mines

A variety of bear activity types were recorded at sites visited in the field (Figure I.3), denoting the opportunistic feeding habits of bears and the fact that some individual bears were more carnivorous whereas others primarily herbivorous. Sample sizes (number of sites with a specific activity) differ for each activity, with the primary activity recorded being bedding (resting) followed by feeding on ungulate carcasses and digging for plant roots. Rodent digging, feeding on ants and tree marking (tree rubbing and claw marking) were only recorded at 12–15 sites each.

Most bear activity I recorded was outside mine leases (>60% with the exception of herbaceous feeding), reflecting my sampling regime biased towards visiting GPS location clusters, more of which formed outside mines compared to on mine sites. Reclaimed mines had more bear activity than the active Cheviot MSL and no activity on the Cheviot pits, a pattern in accordance to low bear home range overlap with Cheviot MSL as compared to reclaimed mines. Also in accordance to higher proportions of bear home range overlap compared with the other mine leases, Luscar MSL had the highest percentage of bear activity of all mines. Feeding on ungulates and root digging in particular appear to be occurring more on Luscar than on the other mine leases. The one exception to this pattern was herbaceous feeding which appears to occur in equal proportions on Luscar and Gregg River MSLs and outside mines, when the data are pooled across seasons. I suspect that herbaceous feeding actually occurs preferentially on reclaimed mines, but unfortunately small sample sizes for this activity preclude seasonal analyses. No instance of berry feeding was recorded on mine leases, which is likely a reflection of low availability of berries on MSLs (Chapter 4). The lack of records of berry feeding on mines is consistent with the pattern of small proportion of home ranges overlapping mines in late hyperphagia, when berry feeding typically occurs.

Bedding and Ungulate Kill Site Selection

On Luscar MSL, bears selected forested (undisturbed) habitat and avoided grassland and barren land for bedding (Luscar MSL: standardised selection ratios $\beta_{forest} = 0.841$, $\beta_{grassland} = 0.071$, $\beta_{barren} = 0.087$). The same pattern was observed for Gregg River MSL, except that barren land actually was selected by bears for bedding (Gregg River MSL: standardised selection ratios $\beta_{forest} = 0.494$, $\beta_{grassland} = 0.110$, $\beta_{barren} = 0.396$). Barren land on Gregg River MSL is found primarily on rock walls of old pits often reclaimed to freshwater lakes. Statistically, apparent bed-site selection of barren land is unreliable and likely a product of small sample sizes resulting in high standard errors. Biologically, given that the highest home range overlap for this MSL occurs in early hyperphagia (summer), bears may bed on barren land so that they can access water quickly.

Ungulate consumption sites on reclaimed mines were selected for primarily in forested areas, with grassland and barren land areas being negatively selected (Luscar MSL: standardised selection ratios $\beta_{forest} = 0.906$, $\beta_{grassland} = 0.037$, $\beta_{barren} = 0.057$; Gregg River MSL: standardised selection ratios $\beta_{forest} = 1$, $\beta_{grassland} = 0$, $\beta_{barren} = 0$). Forests may provide more suitable cover for stalking and predating on ungulates compared to open habitats where predators are easier to detect. Hunting strategies that make use of forest cover and potentially habitat edges (the influence of which will be tested in future analyses) may be favoured by predators other than bears as well. After a kill is made by cougars (*Puma concolor*) (Murphy et al. 1998) or wolves (*Canis lupus*) (Wilmers et al. 2003), grizzly bears may displace these predators from ungulate kills. Indeed, scavenging is an important part of bear diet in my study area (Chapter 5).

Cheviot Haul Road Crossings

Maintaining habitat connectivity is essential for long-term persistence of wildlife species with wide-ranging requirements such as large carnivores (Chetkiewicz et al. 2006). Roads and high traffic volumes can be major barriers to animal movement and can impede genetic flow between populations thereby affecting population fitness. Intensive monitoring of bear movement using GPS radio collar technologies revealed that bears do cross the active haul road and allowed me to identify sections of the road with high frequency of crossings. Most road crossings occurred during early hyperphagia and especially in the northern sections of the road, in areas where the road crosses Luscar MSL (Figure I.4). On this reclaimed mine public access is restricted to designated trails only and bears graze on vegetation and kill ungulates on the lease. In late hyperphagia, another area where crossings were concentrated was 500 m north of Prospect Creek's junction with the McLeod River. Few crossings occurred in the southern sections of the road possibly because the Cheviot haul road and active pits couple with motorised public access along a county road that follows the McLeod River and crosses the Cheviot MSL. However, one bear crossed the haul road on Cheviot MSL on several occasions, moved near the mine offices and made two ungulate kills in an undisturbed patch of forest at the centre of the active mining operations.

Bear Use of Areas near Mine Trails

In Alberta, most human caused grizzly bear mortalities occur within 500 m of a road or human use trail. Opening of roads and trails facilitates human access into previously remote areas and increases the chance of human–bear interactions. Of all trail types and seasons, non-motorised trails in early hyperphagia had the highest occurrence of bear locations (Figure I.5). Early hyperphagia is the time of the year when bears graze on forbs and kill ungulates on reclaimed MSLs, whereas in late hyperphagia bears move outside MSLs to feed on berries. For motorised and non-motorised trails, I found that late hyperphagia is the season with the lowest occurrence of grizzly bear locations along trails. Late hyperphagia also corresponds to the ungulate hunting season, when trails receive high levels of motorized traffic. Future analyses based on precise quantification of human use of access trails will allow an assessment on whether the seasonal difference in food availability or the difference in intensity of human use of trails is the key driving factor for grizzly bear occurrence along trails.

CONCLUSIONS

Grizzly bears have recolonised, forage and rest on reclaimed open pit coal mines in west-central Alberta. The proportion of bear home range overlap with reclaimed MSLs was highest in spring/early summer (hypophagia and early hyperphagia). Luscar MSL had the highest proportion of bear home range overlap followed by Gregg River MSL, whereas Cheviot MSL had the lowest, indicating that bears may select reclaimed mines while avoiding active mining operations. On reclaimed MSLs, bears graze on vegetation and kill ungulates, with kills found primarily in forested areas and few carcasses out in vast open areas which dominate reclaimed mines. Reclaimed mines provide not only forage but also resting habitat opportunities for bears with bed sites occurring primarily at the shelter of original tree patches undisturbed during the active mining phase. This finding along with the spatial distribution of ungulate carcasses consumed by bears suggest that if the management objective is to enable bear use of reclaimed mines then large original forest patches should be maintained in mine planning.

High risk of human-caused mortalities associated with expansion of access into previously remote areas is a major threat to the long-term viability of grizzly bears (Nielsen et al. 2004b). Conflicts may arise along roads used for mining activity or along recreational trails used by the public. Although I have not recorded any bear mortality resulting from collision with haul road traffic, bears cross the active Cheviot mine haul road primarily at its northern sections suggesting that the potential for collision exists. I intuitively suspect that enforcing speed limits along the haul road particularly in spring and summer when crossings are the most frequent will decrease the likelihood of road mortality. Any users of mine haul roads should be informed about the risk of wildlife crossing the roads and road warning signs should signal areas where crossings are most likely to occur. Proper waste management practices will help prevent attracting bears to mine buildings and storage compounds thus decreasing the chance of conflict during active mining.

Given that bears use reclaimed mines in spring and early summer, conflict prevention strategies should involve human access management by allowing access along designated trails only. During early hyperphagia, when bear home ranges have the largest overlap with mine leases, human access can be temporarily prohibited by closure of trails with high risk of conflict. Bear warning signs could be installed at trail heads to inform the public about the risk of bear encounters and should include recommendations on carrying a non-lethal deterrent such as bear spray. These signs should be left along trails for all bear active seasons, because although lower, the risk of encounters still exists for fall (late hyperphagia). Lack of access regulations would expose the public to an increase in chances of bear encounters resulting in an increase in the probability of conflict.

Educating active haul road users about the potential for collisions with wildlife, regulating access along recreational trails, preserving undisturbed forest patches and ideally restoring the original (forested) vegetation cover will help mitigate the effects of mining development on grizzly bears.

LITERATURE CITED

Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management **59**:584-594.

Alberta Grizzly Bear Recovery Team. 2008. Alberta Grizzly Bear Recovery Plan 2008-2013. [online] URL: http://www.srd.alberta.ca/fishwildlife/wildlifeinalberta/grizzlybearmanagement/default.aspx

Ale, S. B., and C. J.Whelan. 2008. Reappraisal of the role of big, fierce predators! Biodiversity Conservation **17**:685-690.

Benn, B., and S. Herrero. 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971–1998. Ursus **13**:213-221.

BWT. 2010. Cheviot and Luscar mine Wildlife Inventory 2009. Created for Teck Coal Limited, Cardinal River Operations, by Bighorn Wildlife Technologies Ltd., Hinton, AB, Canada.

Chetkiewicz, C-L.B., C. C. St. Clair, C.C. and M. S. Boyce. 2006. Corridors for conservation: Integrating pattern and process. Annual Review of Ecology, Evolution and Systematics **37**:317-342.

Government of Alberta (2010) Status of the grizzly bear (*Ursus arctos*) in Alberta. [online] URL: http://srd.alberta.ca/biodiversitystewardship/speciesatrisk/DetailedStatus/documents/Status-GrizzlyBear-inAlberta–Feb2010.pdf.

Grizzly Bear Inventory Team (2007) Alberta DNA population estimate reports 2004–2007. [online] URL: http://www.srd.alberta.ca/ManagingPrograms/FishWildlifeManagement/BearManagement/GrizzlyBears/GrizzlyBears.aspx.

Jansen, B.D., P. R.Krausman, K. D. Bristow, J. R. Heffelfinger, and J. C. deVos Jr. 2009. Surface mining and ecology of desert bighorn sheep. Southwestern Naturalist **54**:430-438.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data:

theoretical motivation and evaluation methods. Journal of Wildlife Management **70**:347-357.

Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. Biological Conservation **81**:161-177.

Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. Journal of Mammalogy **87**:1112-1121.

Murphy, K. M., G. S. Felzien, M. G. Hornocker, and T. K. Ruth. 1998. Encounter competition between bears and cougars: some ecological implications. Ursus **10**:55-60.

Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004a. Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management **199**:51-65.

Nielsen, S. E., S. Herrero, M. S. Boyce, R. D. Mace, B. Benn, M. L. Gibeau, and S. Jevons. 2004b. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biological Conservation **120**:101-113.

Servheen, C., S. Herrero, and B. Peyton (1999) Status survey of the bears of the world and global conservation action plan. IUCN, Gland, Switzerland.

Tardiff, S. E., and J. A. Stanford. 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology **79**:2219-2228.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10**:964-976.

Weir, J. N., S. P. Mahoney, B. McLaren, and S. H. Ferguson. 2007. Effects of mine development on woodland caribou *Rangifer tarandus* distribution. Wildlife Biology **13**:66-74.

Willson, M. F., and S. M. Gende. 2004. Seed dispersal by brown bears, *Ursus arctos*, in Southeastern Alaska. Canadian Field Naturalist **118**:499-503.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology **72**:909-916.

Table I.1: Adult grizzly bears monitored in 2008–2010 on and around coal mineral surface leases (MSLs) in west-central Alberta, Canada.

Bear ID	Sex	Years Monitored	GPS Locations on Luscar MSL	GPS Locations on Gregg River MSL	GPS Locations on Cheviot MSL
G023	Female	2	1,734	440	0
G037	Female	1	245	1,280	0
G053	Male	1<	43	5	0
G110	Male	2	0	0	71
G111	Female	3	299	341	204
G112	Male	1	315	219	4
G113	Female	2	1,245	19	0
G115	Male	2	556	655	0
G117	Female	2	0	0	228
G118	Female	1	273	229	0

During May–November 2008–2010 I visited 573 GPS locations used by bears on Luscar MSL (n_{L} = 113), Gregg River MSL (n_{GR} = 57), Cheviot MSL (n_{C} = 13) and outside mines (n_{OM} = 390)

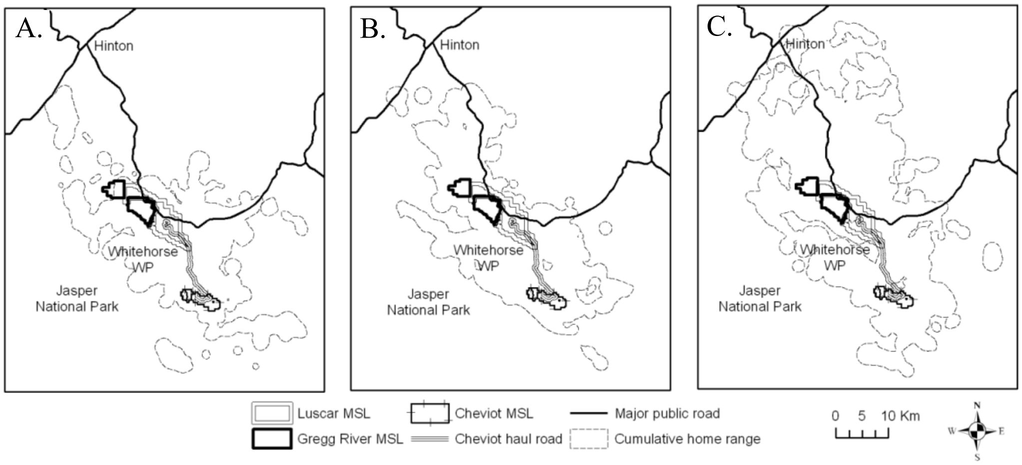

Figure I.1: The study area in west-central Alberta, Canada included open pit mine leases, protected areas and public lands. Cumulative grizzly bear home ranges for three seasons were generated by merging 95% fixed kernels of individual radio collared bears across the 2008–2010 monitoring period: A. Hypophagia (spring), B. Early hyperphagia (summer) and C. Late hyperphagia (fall).

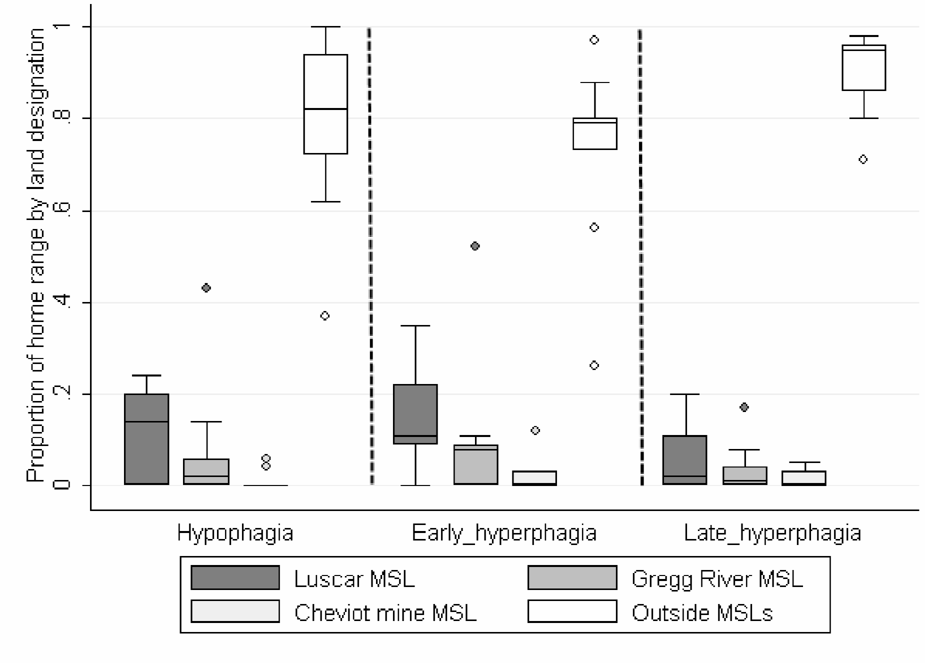

Figure I.2: Proportion of grizzly bear home ranges (95% fixed kernels) overlapping with mine leases and areas outside mines by season. Data are for 10 grizzly bears monitored in 2008–2010 on and around reclaimed (Luscar MSL; Gregg River MSL) and active (Cheviot MSL) open pit coal mines in west-central Alberta.

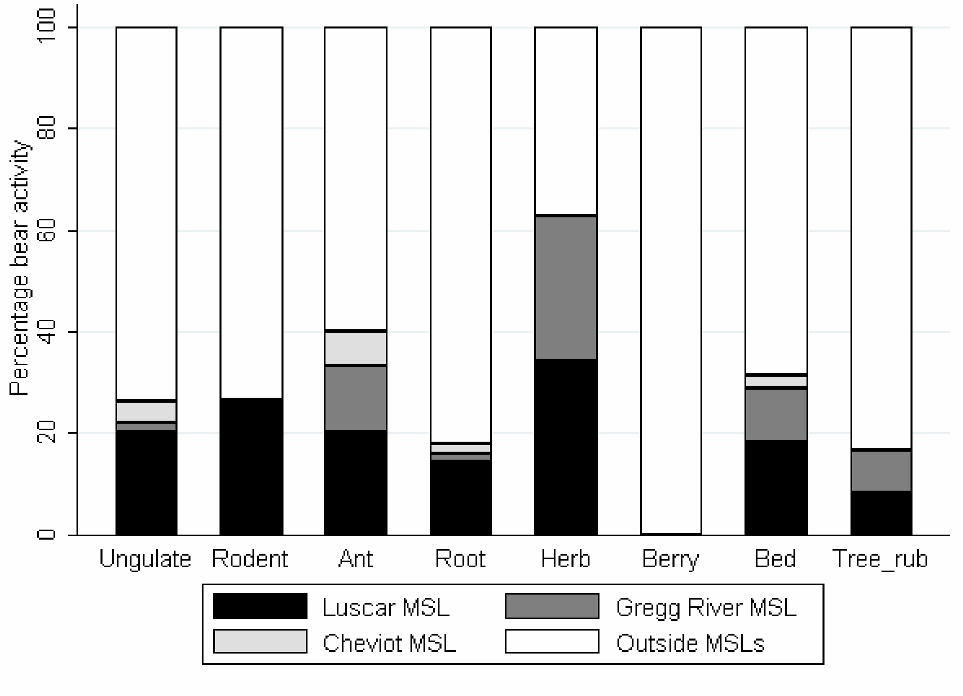

Figure I.3: Percentage bear activity on mine leases and areas outside mines by season, based on 573 bear-used locations visited by field teams. Data are pooled across seasons for 10 grizzly bears monitored in 2008–2010 on and around reclaimed (Luscar MSL; Gregg River MSL) and active (Cheviot MSL) open pit coal mines in west-central Alberta.

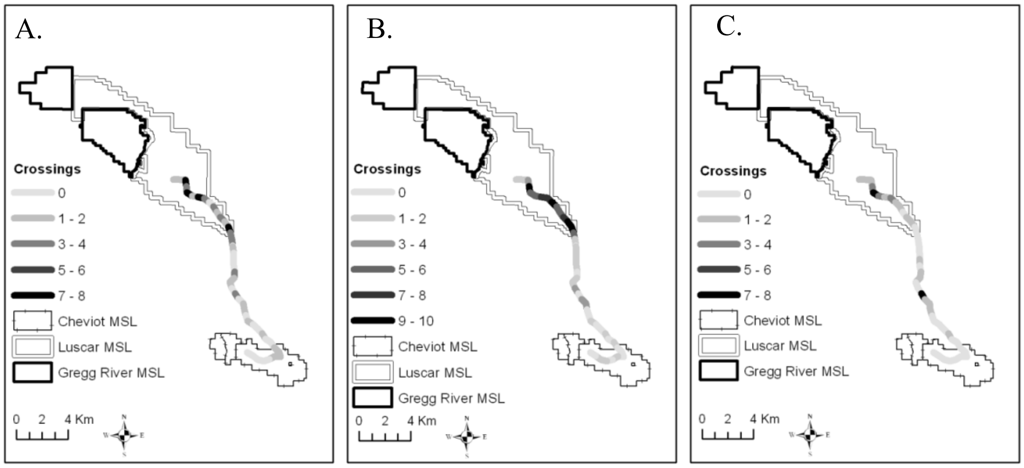

Figure I.4: Frequency of Cheviot coal mine haul road crossings by radio collared grizzly bears in 2008–2010, by season. High crossing frequency is given in darker shades of grey. The haul road was active 24 h/day during the period of grizzly bear monitoring. A. Hypophagia (spring), B. Early hyperphagia (summer) and C. Late hyperphagia (fall).

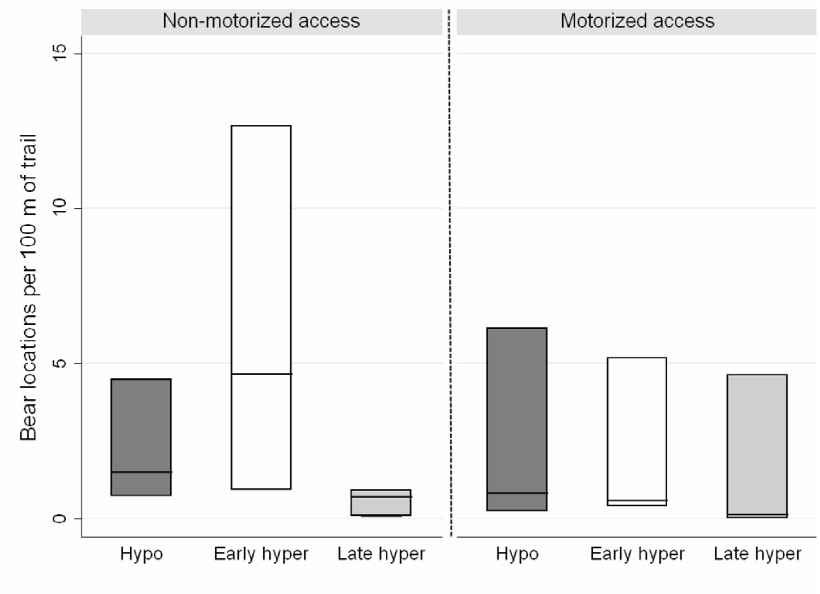

Figure I.5: Occurrence of grizzly bears in a 500 m buffer along designated access trails on Luscar and Gregg River reclaimed MSLs. Each box plot represents one season (hypophagia, early hyperphagia and late hyperphagia) and the data are split by non-motorised (n_1 = 3) and motorised (n_2 = 3) access trails. Occurrence data are from GPS radio collared bears monitored during 2008–2010 in west-central Alberta.

APPENDIX 2

ECOLOGICAL EFFECTS OF MINE RECLAMATION ON GRIZZLY BEARS

ABSTRACT

The grizzly bear (*Ursus arctos*) is a threatened species in Alberta and little is known about the response to coal mine reclamation by bears. I addressed basic ecological questions to describe landscape change effects on grizzly bears, focusing on Luscar and Gregg River reclaimed coal mines in west-central Alberta as case studies. I summarize bear use of mineral disturbance limits in relation to season, habitat, diet, and designated human access trails. Eight adult bears were monitored intensively during 2008-2010 using GPS radiocollars that allowed tracking of their occurrence on the landscape and facilitated collection of scats for diet analysis. Bears were present on reclaimed mines mostly during summer and fed primarily on vegetative matter. Although habitats were similar on the two mines under study, on Luscar mine bears had higher use of undisturbed forested areas and were closer to edge than on Gregg River mine. I attribute these difference primarily to higher presence of humans along designated access trails on Luscar mine, but bears responded differently to motorized and non-motorized trails. While reclaimed mines can provide habitat and forage for grizzly bears in the summer, maintaining undisturbed forest patches and access management are necessary to facilitate bear persistence on a reclaimed landscape.

INTRODUCTION

One of the major goals of mine reclamation is provision of habitat for wildlife (Erickson 1995). In North America including Alberta ungulates are typically chosen as target species for assessing reclamation success (MacCallum 2003). On predominantly open landscapes characteristic of reclaimed mines ungulates are readily visible and can be surveyed through direct observations, with surveys replicated along years (BWT 2010). Because of their naturally lower population numbers and often secretive behaviour, carnivores are used less commonly as indicators of reclamation outcome. Surveys that do focus on carnivores typically rely on snow cover to record occurrence based on tracks, sometimes supplemented by opportunistic direct observations. Following an animal's path in the snow can provide information on behaviour but is highly effort intensive and restricted to winter, early spring and late fall. For bear species which spend most of winter denning, such data are not generally appropriate. Remote cameras are other tools useful for monitoring occurrence which have the advantage of not requiring snow cover. While such data do provide basic information on occurrence, they supply relatively little information on animal behaviour because of the stationary/localized type of data they collect. More informative data collection schemes are possible but involve careful designs requiring a large number of camera stations.

Recent advances in wildlife monitoring technology allow tracking of mammalian species day and night and across seasons. GPS radiocollars can be programmed to acquire a relocation at the rate desired by the investigator providing ample insights into animal occurrence on the landscape. These devices are particularly suited for monitoring wide ranging species which may be important from a reclamation standpoint but are otherwise difficult to monitor. The grizzly bear is such a species because of large home range sizes and ecological role in seed dispersal, soil aeration (Tardiff and Stanford 1998), nitrogen exchange (Gende et al. 2002) and ungulate population limitation (Zager and Beecham 2006). This species' range has experienced range contraction in North America because of human persecution and landscape conversion (Laliberte and Ripple 2004). While grizzly bears can still be found in large numbers in British Columbia, in the neighbouring province of Alberta grizzly bears are at the eastern edge of the species' distribution for southern Canada. In 2010, the grizzly bear was designated as Threatened in Alberta in response to estimated low population numbers resulting from legal harvest and increased illegal shooting associated with habitat conversion enabling human access in previously undisturbed areas (Alberta Grizzly Bear Recovery Team 2008).

Many of the coal mining operations in Alberta occur in areas inhabited by grizzly bears, where the predominant land cover is boreal forest. Following closure of mining, reclamation results in habitat change, from forest to predominantly open landscapes resembling grasslands. Re-vegetated mined lands have low vegetative species richness compared to neighbouring undisturbed lands, as species sown as part of reclamation are typically selected to improve wildlife forage, primarily for ungulates. Because grizzly bears have a mixed diet which includes herbaceous vegetation acquired through grazing, reclaimed mines can potentially provide foraging opportunities for bears. In addition, ungulate use of grasslands on reclaimed mines may also attract bears to these areas.

To document ecological effects of reclamation on grizzly bears, I monitored grizzly bears for 3 years to assess if bears used reclaimed mines or avoided them, and whether use of mines was confined to certain seasons. If bears did use mines, my goal was to identify the type of habitats where bears occurred, differentiating between reclaimed (disturbed) and original (undisturbed). Lastly, I was interested in qualitatively assessing bear diet on reclaimed mines and investigating the influence of human access on bear occurrence. The descriptive results of these assessments are presented in comparison for 2 reclaimed mines chosen as case studies.

METHODS

Study Area

Data collection occurred on Luscar and Gregg River reclaimed open-pit coal mines located at the interface between the eastern slopes of the Rocky Mountains and foothills of west-central Alberta. The study area extent was confined to the mineral disturbance limit (hereafter, MDL) of each of the two mines (Figure II.1). These limits included actual disturbance (mined land reclaimed to grassland, and pit walls terraced to provide bighorn sheep [*Ovis* *canadensis*] escape terrain [(MacCallum and Geist 1992)]) and undisturbed area (forest left untouched during active mining). MDL areas are part of the larger mineral surface leases (hereafter, MSLs). Luscar mine leased by Teck Coal had a total MDL area of 25.9 km^2, 7.7% of which included undisturbed original forest present in patches in a matrix dominated by grassland reclamation. The disturbance included an area of 16.8% supporting active operations at a mine office, shop, processing plant and haul road. Gregg River mine leased by Sherritt Coal had a total MDL area of 15.8 km^2, 6.1% of which was comprised of undisturbed tree patches. No active pit blasting or coal extraction occurred at either of the mines during the study.

Reclamation to grasslands at Luscar and Gregg Rive mines involved a mixture of plants dominated numerically by clovers (*Melilotus* spp., *Trifolium* spp.), alfalfa (*Medicago* spp.), milkvetch (*Astragalus* spp.), dandelion (*Taraxacum* spp.) and Graminoids. All these represent potential forage for wildlife. Ungulates including bighorn sheep, elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) used the MDL area of both mines year-round. In addition to grizzly bears, other large carnivore species in the area were black bear (*Ursus americanus*), wolf (*Canis lupus*) and cougar (*Puma concolor*).

Recreational human access was restricted to motorized and non-motorized designated trails and no hunting occurred within the mine MSLs. ATV-ing and hunting were common recreational activities outside mine leases, with recreationists using designated trails that crossed MDL areas primarily in the summer and fall.

Monitoring

In 2008-2010, with assistance from the Foothills Research Institute Grizzly Bear Program (Hinton, Alberta), I set Televilt Telus UHF (Followit, Lindesberg, Sweden) GPS radiocollars on 12 adult grizzly bears captured using culvert traps, limited leg-hold snaring and helicopter darting within and in the vicinity of MDLs. Two of these bears pulled off their collars within a month from capture and 2 other bears did not use the reclaimed area under study. The remaining 8 animals used MDL areas and represented my sample size for assessing bear response to mine reclamation. Collars were programmed to acquire a relocation every hour during March 15-December 1, 24-h a day, when bears were mostly outside winter dens. GPS relocations acquired at bear capture sites and from winter dens were excluded from all calculations. Every 4-5 week period I approached each bear on the ground or from the air and triggered its collar to send data remotely via VHF to my radio receiver unit. This enabled me to select relocations used by bears for field visitation to collect scat for diet analysis. Spatial analyses described below were carried out in ArcGIS v.9.2 and v.10 (ESRI, Redlands, California), and diet analyses were carried out in the lab. An in-depth description of data collection protocols is available in Cristescu (2012).

Space Use by Bears

In previous work I documented proportion of grizzly bear home ranges overlapping Luscar and Gregg River MSLs (Cristescu et al. 2011). Herein I use the spatial distribution of all GPS collar relocations to describe seasonal occurrence of grizzly bears within MDLs, differentiating between three seasons relevant to bear feeding in the study region: spring ("hypophagia"; den emergence to June 14), summer ("early hyperphagia"; June 15 to August 7) and fall ("late hyperphagia"; August 8 to den entrance) (Nielsen et al. 2004). In addition, for each season I describe bear occurrence in disturbed (forest) versus undisturbed (grassland and barren) areas within MDLs and compute the distance from each GPS relocation to the nearest edge. I define "edge" as the boundary area between the two above mentioned habitat categories.

Bear Diet

Diet analysis methods are described in detail in (Schwab et al. 2011). In brief, I collected grizzly bear scat whenever I came across it at GPS relocations visited on MDL areas. Scat samples were frozen to preserve them until further analyses in the lab. Following autoclaving a 30 mL sample was extracted from each scat and analyzed for diet contents under a dissecting microscope. Herein I describe frequency of occurrence of each major food item in scats collected within MDLs. Major items were classified as herbaceous vegetation, other plant material (root and berry), mammal (ungulate and small mammals) and insects (primarily ants). More detailed analyses involving biomass estimates for specific foods ingested by bears and a comparison with bear diet in un-mined areas are provided in Chapter 4.

Response of Bears to Human Access

We report the distance from each GPS collar relocation to the nearest designated access trail crossing MDLs under study, differentiating between motorized and non-motorized trails. Separate calculations were carried out for each season because bears may respond differently to trails according to time of the year, in relation to seasonal variation in human access. Preliminary analyses of motion camera data show highest motorized access in the summer, primarily from recreational ATV users, and high non-motorized access in the fall, mainly from hunters.

RESULTS

Space Use by Bears

Grizzly bears used Luscar and Gregg River MDL areas in all seasons. During the 2008-2010 monitoring period I obtained a total of 4,342 bear GPS radiocollar relocations within the study area extent (Table II.1). Although the total number of bear relocations was relatively similar between the two mines, Luscar MDL had a 1.6 higher spatial extent compared to Gregg River MDL suggesting higher use of the latter by the bears monitored in this study.

Seasonally, occurrence of bears on both MDL areas was highest in the summer (Figure II.2). The maximum number of bears occurring in any one season by MDL was documented for Luscar MDL (*n* = 7; summer), while the minimum occurred for Gregg River MDL (*n* = 4; fall). Half of all radiocollared bears (*n* = 4) were monitored for ≥2 years and all used Luscar MDL in multiple years during spring and summer. Correspondingly, two bears used Gregg River MDL in the spring and summer of multiple years. MDL areas were used in the fall of multiple years by a single bear. The only bear monitored for three consecutive years used both MDL areas in all years in the summer.

Irrespective of season, bears used undisturbed (treed) and disturbed (non-treed) areas within both MDL areas. With the exception of summer, use of treed areas occurred in higher proportion on Luscar MDL than on Gregg River MDL, although the two mines had highly similar treed to non-treed area ratios (Luscar MDL 0.08; Gregg River MDL 0.06) (Figure II.3). Bears on Luscar MDL used treed areas to the highest extent in the fall, a season when bears on Gregg River MDL used treed areas to the least extent.

On Luscar MDL GPS relocations occurred closer to the edge between disturbed area and tree islands compared to Gregg River MDL (Figure II.4). As seasons progressed bears used areas further from edge, with the exception of bears using Gregg River MDL in spring. During this season bears on Gregg River MDL were on average two times further from edge than bears on Luscar MDL.

Bear Diet

Of the 59 grizzly bears scats collected in 2009 and 2010 (Luscar MDL *n* = 31; Gregg River MDL *n* = 28), for both MDL areas an average scat contained primarily vegetative material grazed by bears. Herbaceous material occurred at higher frequency in samples collected on Gregg River MDL compared to Luscar MDL (Figure II.5). Plant foods other than herbaceous (i.e., roots and berries) occurred on average 3.4 times more on Luscar MDL than on Gregg River MDL. Mammals and insects occurred in relatively similar proportions in scats collected on the two mines.

Response of Bears to Human Access

On both MDL areas, bears were furthest from non-motorized trails in the fall (Figure II.6). On Luscar MDL which had motorized trails, bears were furthest from these in summer. For both MDLs, bears were closest to trails during spring, with the exception of non-motorized trails on Luscar MDL.

DISCUSSION

Grizzly bears used Luscar and Gregg River MDL areas in all seasons, with the peak use occurring in summer. During this season, grazing material sown as part of reclamation was highly available within MDLs attracting wildlife including ungulates and grizzly bears. However my data show throughout the year bears spent overall most time outside mined areas, which suggests that vast areas with no mining disturbance are required for bear population persistence. In spring, bears dig sweet vetch (*Hedysarum* spp.) roots outside mines whereas in the fall huckleberries (*Vaccinium* spp.), Canada buffaloberry (*Sheperdia canadensis*) and crowberry (*Empetrum nigrum*) are major foods consumed in preparation for winter denning (Chapter 4). Ungulates are consumed on and outside MDLs but they occur substantially more in the diet of bears outside mines (Chapter 4). Ungulate risk of predation is likely low on the largely open areas characteristic of reclamation. Given that bighorn sheep, elk and mule deer populations have been increasing on mines (BWT 2010), MDL areas likely act as sources of ungulates for the surrounding landscape.

Original tree patches left undisturbed during mining were highly used by bears especially on Luscar MDL. Such patches may serve multiple roles including providing thermal cover during bedding and hunting opportunities for predatory bears seeking ungulates. Bears have poor ability to thermoregulate and maintaining forested areas which provide shade may be important during hot summer days. Tree cover also may prevent body heat loss from atmospheric precipitation on cold days. With regards to ungulate predation, field confirmed ungulate carcasses used by bears in 2009-2010 within MDL areas were located at the shelter of forest (Chapter 5). In addition to being important for bears, tree patches likely have functional value for other mammals. For example, I often located ungulate rub trees and bedding sites on tree islands within MDLs.

Patches of original forest also supply native plant dispersers that can colonize reclaimed areas. Their role as dispersal reservoirs can facilitate ecological succession from non-native clovers, alfalfa and dandelion to a community dominated by native vegetation. However, this process is lengthy in harsh mountainous environments (Smyth 1997) such as in my study and it is unlikely that introduced species would be completely replaced. On the contrary, these plants are spread by wildlife through direct consumption or attachment to their bodies when travelling through non-native grassland areas within MDLs. A more ecologically sound approach to reclamation is to use native plant species, such as currently under way at Teck's nearby Cheviot operation.

Our calculations of distance to nearest habitat edge confirm the importance of tree cover for bears on mined areas. Seasonal differences and overall lower distance to edge on Luscar compared to Gregg River MDL point to variation in feeding on the two MDLs as well as potential influence of human use. Although frequency of mammalian food items in bear scat was relatively similar on the two MDLs, my field visitation of GPS relocations showed a higher number of ungulate carcasses consumed by bears on Luscar MDL, located within tree islands near the grassland edge (Chapter 5). On Luscar MDL bears used tree islands extensively and were closest to edge in spring, a season during which many bears exhibited predatory behaviour in response availability of ungulate calves and lambs. On Gregg River MDL where bears were less predatory, spring relocations were furthest from edges than in any other season.

On the other hand, grizzly bears may have been using areas closer to edge on Luscar MDL because edges may be perceived as secure by this species (Nielsen et al. 2004). Luscar MDL had higher human activity (larger number of recreational access trails and mining operations). However, overall levels of mining activity were similar across seasons, whereas human use of mine trails differed. Human access along motorized trails peaked in summer, while in fall non-motorized trails received high use by hunters. Bears responded to human activity on Luscar MDL by using tree islands substantially, more so in the fall than any other season. Also in the fall, bears were furthest from non-motorized trails, suggesting an avoidance of hunters. Similarly, on Gregg River MDL bears were furthest from non-motorized access in the fall. However, inferences on bear occurrence in relation to distance to trails for this MDL must be interpreted with caution, as only one designated trail crosses Gregg River MDL. As expected, motorized trails on Luscar MDL were mostly avoided during the summer season of high but unpredictable human use.

RECOMMENDATIONS

Habitat enhancement through mine reclamation can promote use of mined lands by wildlife such as grizzly bears but should be designed to decrease human-caused mortality risk. Maintaining original vegetation cover such as treed areas in this study should be a major goal in mine planning. For areas disturbed by active mining, native plants are excellent alternatives to non-native species and can be used to achieve the same goal of wildlife colonization on MDLs. Planting sweet vetch and berry shrubs on mines may promote increased grizzly bear use of these areas in spring and fall but such attractants may work against long-term goal of promoting grizzly bear population viability. Even in the absence of legal hunting within MDLs, risk of illegal shooting on these predominantly open areas may be greater in the fall when many trail users carry firearms. Access management is a key component of bear population recovery (Alberta Grizzly Bear Recovery Team 2008). Strict enforcement of access regulations and firearms regime along designated MDL trails is needed to prevent human-bear conflict.

Wildlife monitoring programs should be implemented not only following reclamation, but during all phases of mining and ideally pre-mining for the proposed MDL area. When detailed behavioural data are required, focalized studies that employ GPS radiocollars provide unmatched resolution in tracking animal movements on the landscape. If detailed data are not essential, then non-invasive techniques such as remote cameras can be used to document trends in wildlife occupancy. Remote cameras have many advantages over other methods, including non-invasiveness, low cost and ability to monitor a variety of species, including human trail users. Monitoring programs with long-term vision will enable key insights, such as use of MDLs by the same individual animals across multiple years, as demonstrated for some of the grizzly bears monitored in this study.

LITERATURE CITED

Alberta Grizzly Bear Recovery Team. 2008. Alberta Grizzly Bear Recovery Plan 2008-2013. [online] URL: http://www.srd.alberta.ca/fishwildlife/wildlifeinalberta/grizzlybearmanagement/default.aspx

BWT. 2010. Cheviot and Luscar mine Wildlife Inventory 2009. Created for Teck Coal Limited, Cardinal River Operations, by Bighorn Wildlife Technologies Ltd., Hinton, AB, Canada.

Cristescu, B., G. B. Stenhouse, M. Symbaluk, and M. S. Boyce. 2011. Land-use planning following resource extraction – Lessons from grizzly bears at reclaimed and active open-pit mines. In eds. A.B. Fourie, M. Tibbett, and A. Beersing: Mine Closure 2011− Proceedings of the Sixth International Conference on Mine Closure. Australian Centre for Geomechanics, Nedlands, Australia.

Erickson, D. L. 1995. Policies for the planning and reclamation of coal-mined landscapes: An international comparison. Journal of Environmental Planning and Management **38**:453-467.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience **52**:917-928.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience **54**:123-138.

MacCallum, B. 2003. Reclamation to wildlife habitat in Alberta's Foothills. In eds. W. Price, W. Gardner, and C. Howell: Proceedings of the 27th annual British Columbia mine reclamation symposium, Kamloops BC, September 15-18, 2003. The British Columbia Technical and Research Committee on Reclamation. Bitech Publishers Ltd., Richmond, BC, Canada.

MacCallum, B. N., and V. Geist. 1992. Mountain restoration: Soil and surface wildlife habitat. GeoJournal **27**:23-46.

Nielsen, S. E., M. S. Boyce, and G.B. Stenhouse. 2004. Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management **199**:51-65.

Schwab C., B. Cristescu, J. M. Northrup, G. B. Stenhouse, and M. Ganzle. 2011. Diet and environment shape fecal bacterial microbiota composition and enteric pathogen load of grizzly bears. PLoS ONE **6**:e27905.

Smyth, C.R. 1997. Early succession patterns with a native species seed mix on amended and unamended coal mine spoil in the Rocky Mountains of Southeastern British Columbia, Canada. Arctic and Alpine Research **29**:184-195.

Tardiff, S. E., and J. A. Stanford. 1998. Grizzly bear digging: Effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology **79**:2219-2228.

Zager P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. Ursus **17**:95-108.

Table II.1: Summary of GPS radiocollar relocation data from adult grizzly bears monitored in 2008-2010 on reclaimed coal mine MDL areas in west-central Alberta, Canada.

	GPS relocations on Luscar mine disturbance area				**GPS relocations on Gregg River mine disturbance area**			
	Spring	Summer	Fall	Total	Spring	Summer	Fall	Total
Total	482	1,267	365	2,114	144	1,830	254	2,228

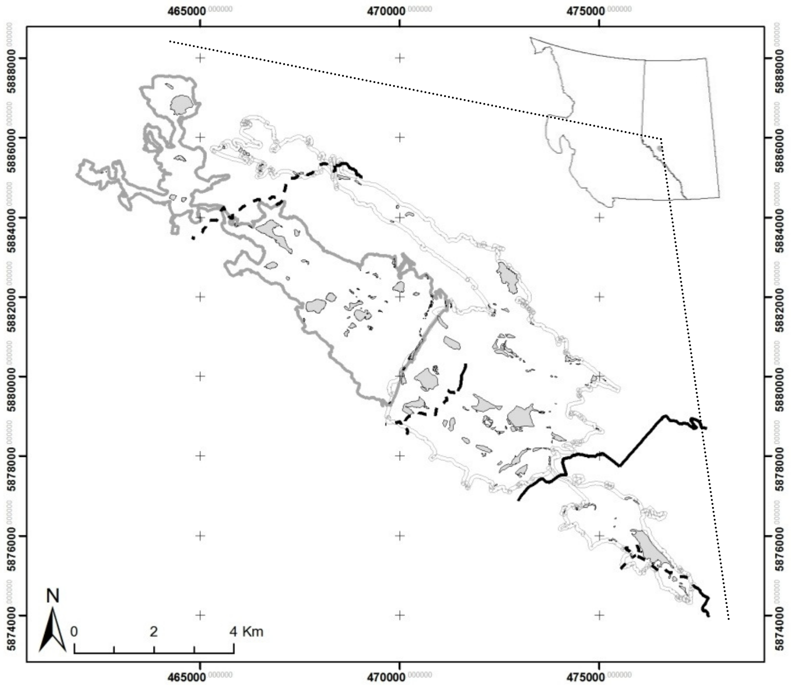

Figure II.1: Study area extent in west-central Alberta showing MDLs for Luscar (double gray line) and Gregg River (single gray line). Gray polygons are tree islands in a matrix of mined land. Solid black lines are motorized and dashed black lines non-motorized trails.

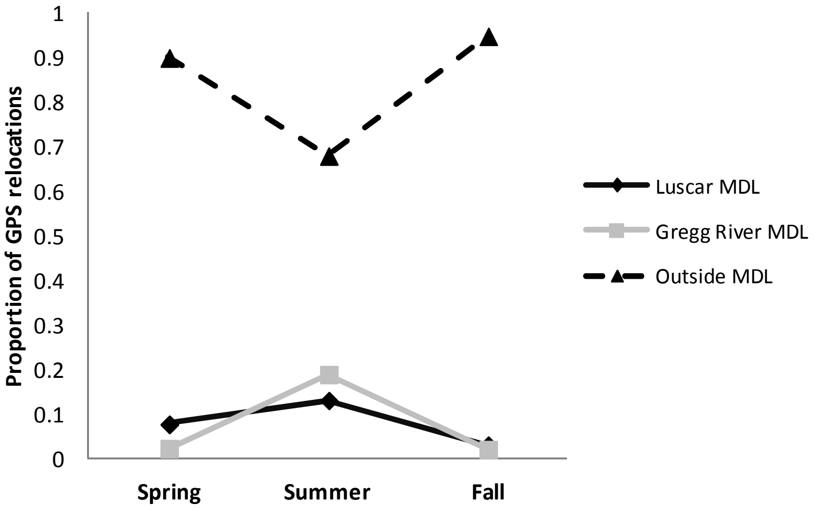

Figure II.2: Proportion of GPS relocations recorded within MDLs and in undisturbed areas neighbouring mined lands. These hourly relocation data provide season-specific relative amounts of time monitored bears used mined and un-mined lands.

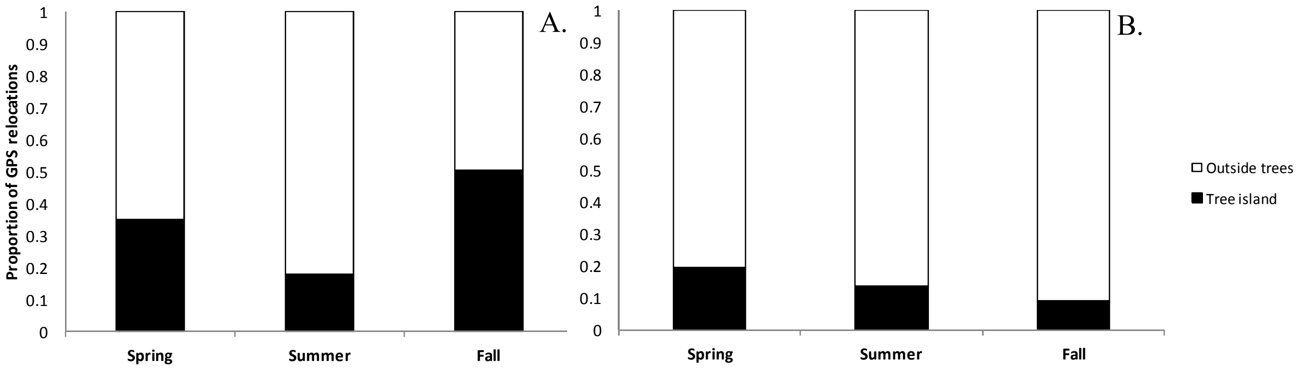

Figure II.3: Proportion of GPS relocations recorded in undisturbed areas (tree islands) versus open disturbed areas (reclaimed grassland and barren) within Luscar MDL (A) and Gregg River MDL (B).

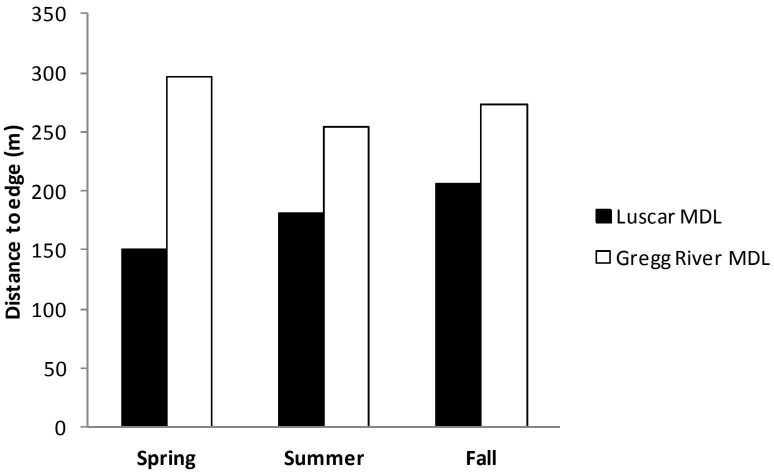

Figure II.4: Mean distance to habitat edge for GPS relocations acquired within MDLs.

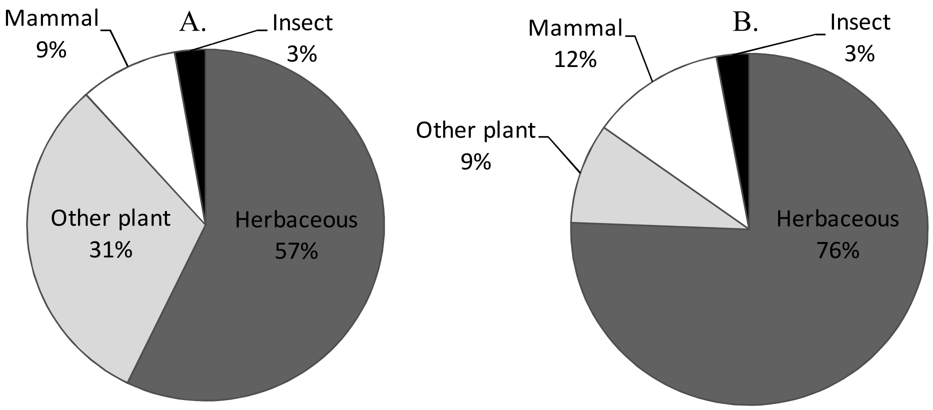

Figure II.5: Frequency of occurrence of broad food items in grizzly bear scats collected within Luscar MDL (A) and Gregg River MDL (B).

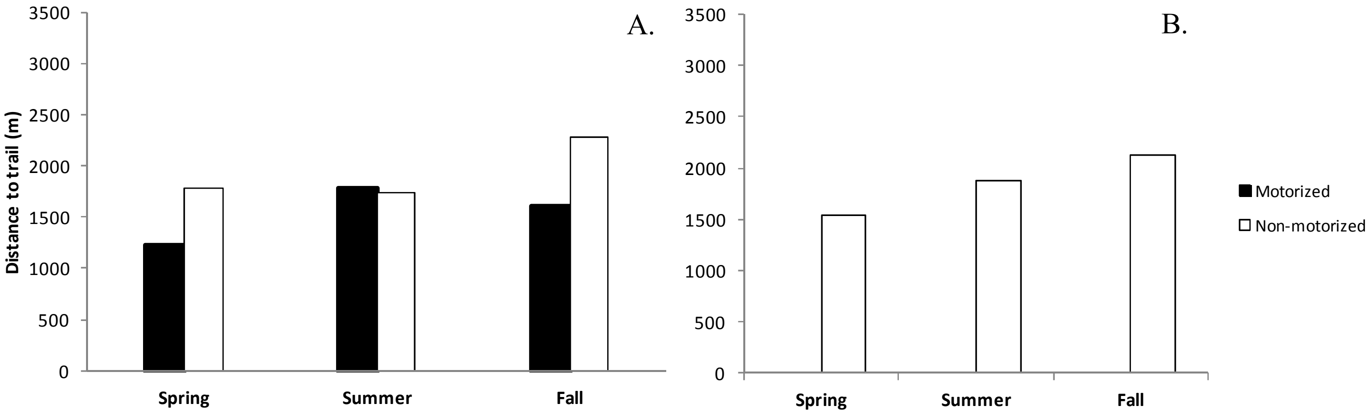

Figure II.6: Mean distance to motorized and non-motorized trails for GPS relocations acquired within Luscar MDL (A) and Gregg River MDL (B).