Photo: Rod Sinclair

A male cougar (*Puma concolor*) after removing its GPS collar in Waterton Lakes National Park.

University of Alberta

Cougar response to roads and predatory behaviour in southwestern Alberta

by

Jeremiah Elbridge Banfield

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

Master of Science
in
Ecology

Department of Biological Sciences

Fall 2012
Edmonton, Alberta

ABSTRACT

In western North America cougar populations are increasing and expanding eastward. Simultaneously, growing human populations are creating new challenges for managers charged with maintaining the viability of cougar populations and their ungulate prey. Information on how cougars respond to human-dominated landscapes and interact with their prey will aid managers in balancing the effects of growing cougar populations with the wishes of growing human populations. Using resource selections functions, I examined cougar responses to roads of varying traffic volumes. Cougars selected rugged terrain presumably to insulate themselves from roads with greater traffic. When assessing impacts of expanding road networks, more attention should be given to roadside topography. Using fine-scale movement and activity data, I examined cougar predatory behaviour. Cougars employed an active stalking style of predation, moving throughout the landscape to locate, stalk, and kill prey. Future models of predator-prey dynamics should consider the cougar’s active style of predation.

AKNOWLEDGEMENTS

First and foremost I would like to acknowledge my supervisor Dr. Mark Boyce; thank you for your support, advice, patience and guidance through my thesis work. More importantly, thanks for bringing me along on several trapping and hunting excursions. To my committee, Nate Webb, Scott Neilsen, David Schindler and Mark Lewis: Thank you for taking the time to make a summer-time defense a reality. A special thanks to Scott Neilsen for working on this during his vacation.

I am grateful to the following agencies for their generous financial and in-kind support, without which this project would never have been possible: Natural Sciences and Engineering Research Council of Canada, Shell Canada; Alberta Conservation Association; Safari Club International-Northern Alberta Chapter; Alberta Sport, Recreation, Parks and Wildlife Foundation, Alberta Sustainable Resource Development, Alberta Parks and Parks Canada.

Numerous individuals from Alberta Sustainable Resource Development and Parks Canada were helpful throughout the duration of my research. Thanks to: Nate Webb, Greg Hale, Perry Abramenko, Kirk Olchowy, Bill Clark, Andrew Gustavson, Bill Dolan and Barb Johnston for providing logistical support, cooperation and sharing information.

I was fortunate to have the support of numerous land and livestock owners in southwestern Alberta. In particular, I’d like to thank my friends Alan and Teri Tapay for teaching me about Alberta cattle and letting me help out with branding. I’m also grateful to Gill Engen for allowing open access to the property he manages.

Without the Italians I don’t think I would have ever finished this project. Thanks to Simone Ciuti and Silvia Simi for your advice, guidance, company, and most importantly friendship.

An integral part of this project was capturing and collaring cougars, which could not have been accomplished without the assistance of my houndsman Brent Sinclair and his faithful pack of hounds. Brent, I am sincerely grateful to have met and worked with you on this project. Our time spent chasing cats will never be forgotten and your friendship is truly unique. Thank you for providing and guiding your hounds, Mag, Dan, Mader, Rosie, Boomer, Sue, Sam, Budweiser, and of course my personal favorite and friend, Katie Mae. No matter where I go or what I do, I will never be as cool as Brent Sinclair.

Thanks to Kyle Knopff for assisting me in my very first capture: And thank you for your advice and tips thereafter.

I am forever indebted to all of my research technicians, Lee Kaiser, Shelby Heistand, Craig Sherwood, Cari Sebright, Kyle Crowson, Marissa Cent and Marcus Mustin. I am honoured to have worked with each of you and cannot thank you enough for your dedication, enthusiasm, patience and overall toughness. The unique qualities and personalities that each of you brought to this project were invaluable, and to say I couldn’t have done it without you is a gross understatement. Thank you very much.

I am grateful for the lifelong friends we made in Pincher Creek, the Simons, Sokownins, Kliens, Butts, and Proudfoots. Thank you for the conversation, laughter and meals. Finally, thanks to my wife, Heather Banfield, for supporting, loving and putting up with me throughout this entire project.

TABLE OF CONTENTS

CHAPTER 1: GENERAL INTRODUCTION

CHAPTER 2: COUGAR RESPONSE TO ROADS: THE INFLUENCE OF TRAFFIC, TOPOGRAPHY, AND LANDCOVER

CHAPTER 3: COUGAR PREDATION BEHAVIOUR: DO COUGARS AMBUSH OR STALK THEIR PREY?

CHAPTER 4: GENERAL CONCLUSIONS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENERAL INTRODUCTION

BACKGROUND

During the early 1900's, cougars (*Puma concolor*) in North America were generally viewed by humans as a danger to livestock and as competition for ungulate game (Sunquist and Sunquist 2002). As a result, cougars were targeted by intense predator control programs and by 1960, heavy human persecution had restricted them to the mountainous regions of western North America (Sunquist and Sunquist 2002). In the 1970s, reclassification from a bountied predator to a game species facilitated a dramatic rebound in western populations (Nadeau 2005) and a subsequent expansion into Midwestern North America (Thompson and Jenks 2005, LaRue et al. 2012).

Over the past 30 years human attitudes toward North American carnivores, including cougars, have shifted (Kellert et al. 1996, Riley and Decker 2000, Decker et al. 2001). Although some still view cougars as a nuisance worthy of extermination, many people recognize their integral place in the larger ecosystem. Despite this recognition, opinions on cougar management range broadly with variations in age, sex, education and geography (Riley and Decker 2000, Davenport et al. 2010).

In both Canada and the US, provincial and state level wildlife agencies are responsible for managing the cougar populations within their respective boundaries. Cougar management, like that for other large carnivores, must balance the needs of the species with the wide range of values and expectations from a diverse public (Decker et al. 2001). Attempting to remain transparent and consistent in their management of cougars, most agencies create management plans, a public document designed to explain and justify population goals, hunting seasons, limits and methods of harvest. Indeed, almost every province and state with existing cougar populations has authored and implemented some form of a cougar management plan (Government of Alberta 1992, Montana Fish Wildlife and Parks 1996, Utah Division of Wildlife Resources 1999, Rachael and Nadeau 2002, Wyoming Game and Fish Department 2006). Similarly, many states and provinces on the cusp of cougar re-colonization have completed (South Dakota Game Fish and Parks 2010) or begun drafting management plans (Government of Saskatchewan 2008, North Dakota Game and Fish Department 2011). While specific population goals and hunting regulations vary between individual provinces and states, common to nearly each plan is the need to sustain cougar populations while also maintaining populations of their ungulate prey (Government of Alberta 1992, Montana Fish Wildlife and Parks 1996, Utah Division of Wildlife Resources 1999, Rachael and Nadeau 2002, Wyoming Game and Fish Department 2006, South Dakota Game Fish and Parks 2010). Although seemingly simple, the consequences of simultaneous growth in human and cougar populations are likely to make this goal more challenging.

Roads networks, for example, will inevitably increase as the growing human population demands more energy and space (Forman et al. 2003, Frair et al. 2008). For cougars, roads act as barriers to movement and dispersal (Dickson et al. 2005), affect home range placement (Dickson and Beier 2002) and are a leading source of mortality (Ruth et al. 2011, Schwab and Zandbergen 2011).

However, little is known about how cougars respond to variation in the traffic associated with roadways. Increasing our knowledge of cougar, road, and traffic relationships will allow wildlife managers to better mitigate the effects of roads under impending human encroachment.

Although the consequences of increasing cougar populations may appear less concerning than those of increasing human populations, cougars can and do have a profound effect on their ungulate prey (Hayes et al. 2000, Rominger et al. 2004). Yet even after decades of research some of the most basic components of cougar predation remain ambiguous. Whether cougars employ an ambush or stalking style of predation, for example, can have implications for functional response models (Holling 1959, Merrill et al. 2011), estimates of kill rate (Knopff et al. 2010, Ruth et al. 2010) and predator-prey dynamics (Kunkel et al. 1999, Pierce et al. 2000, Husseman et al. 2003). However, only anecdotal descriptions of cougar predation behaviours are available (Wilson 1984, Bank and Franklin 1998), and these are subject to observer bias and lack the statistical rigor required for concrete conclusions. A quantitative assessment of cougar predation behavior aimed at inferring the cougars' dominant predatory strategy would improve managers understanding of functional response and cougar-ungulate dynamics.

In the following chapters of this thesis I examine the knowledge gaps outlined above and present my results considering their application to cougar management. I conducted my research in south-west Alberta, where cougars were exposed to an existing network of roads with varying traffic and broad base of ungulate prey.

In chapter 2, I examined how roads of varying traffic volumes influence cougar habitat selection. I fit resource selection functions to GPS location data collected between January 2010 and December 2011 from 12 cougars in south-western Alberta. Traffic volume, estimated as the number of vehicles per hour, was derived from a model incorporating counter data, trail cams and attributes of the surrounding landscape (Northrup et al. 2012). This chapter represents the first study examining cougar response to roads in the context of adjacent landcover, topography, and traffic volume. I present my results and discuss potential management implications.

In chapter 3, I explored cougar predation behavior with the aim of inferring the cougar's dominant predatory strategy. I used fine-scale GPS location data, activity data from radiocollars, and data collected during field visits to GPS clusters to assess cougar predation behaviour. More specifically, I used logistic regression to compare these data at specific time intervals leading up to field-validated kill and non-kill clusters. From my results, I conclude with the cougar's dominant predatory strategy and discuss management implications.

In chapter 4, I make general conclusions and discuss overall management recommendations. I organized chapters 2 and 3 as independent manuscripts intended for separate publication. I formatted chapter 2 for the *Journal of Wildlife Management* and chapter 3 for *Ecology*. For consistency, I similarly formatted the introductory (chapter 1) and concluding (chapter 4) chapters according to the *Journal of Wildlife Management* guidelines.

LITERATURE CITED

Bank, M. S., and W. L. Franklin. 1998. Puma (*Puma concolor patagonica*) feeding observations and attacks on guanacos (*Lama guanicoe*). Mammalia 62:599-605.

Davenport, M. A., C. K. Nielsen, and J. C. Mangun. 2010. Attitudes toward mountain lion management in the midwest: implications for a potentially recolonizing large predator. Human Dimensions of Wildlife 15:373-388.

Decker, D., J., T. Brown, L., and W. Siemer, F. 2001. Human dimensions of wildlife management in North America. The Wildlife Society, Bethesda, Maryland, USA.

Dickson, B. G., and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. Journal of Wildlife Management 66:1235-1245.

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.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Farig, R. France, C. Goldman, K. Heanue, J. Jones, F. Swanson, T. Turrentine, and T. Winter. 2003. Road ecology: science and solutions. Island Press, Washington DC.

Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. Journal of Applied Ecology 45:1504-1513.

Government of Alberta. 1992. Management plan for cougar in Alberta. Alberta Fish and Wildlife Division, Edmonton, Alberta, Canada.

Government of Saskatchewan. 2008. Cougars in Saskatchewan. Saskatchewan Ministry of Environment, Regina, Saskatchewan, Canada.

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

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

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

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

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

Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. Journal of Wildlife Management 63:901-910.

LaRue, M. A., C. K. Nielsen, M. Dowling, K. Miller, B. Wilson, H. Shaw, and C. R. Anderson. 2012. Cougars are recolonizing the midwest: Analysis of cougar confirmations during 1990–2008. Journal of Wildlife Management in press.

Merrill, E., H. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair. 2011. Building a mechanistic understanding of predation with GPS-based movement data. Philosophical Transactions of the Royal Society B-Biological Sciences 365:2279-2288.

Montana Fish Wildlife and Parks. 1996. Management of mountain lions in Montana. Helena, Montana, USA.

Nadeau, S. Idaho mountain lion status report. 2005.

North Dakota Game and Fish Department. 2011. Status of mountain lion management in North Dakota. North Dakota Game and Fish Department, Bismark, North Dakota, USA.

Northrup, J., J. Pitt, T. Muhley, B, 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 in press.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes, effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462-472.

Rachael, J., and S. Nadeau. 2002. Idaho mountain lion management plan. Idaho Department of Fish and Game, Boise, Idaho, USA.

Riley, S. J., and D. J. Decker. 2000. Wildlife stakeholder acceptance capacity for cougars in Montana. Wildlife Society Bulletin 28:931-939.

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

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.

Ruth, T. K., M. A. Haroldson, K. M. Murphy, P. C. Buotte, M. G. Hornocker, and H. B. Quigley. 2011. Cougar survival and source-sink structure on greater Yellowstone's northern range. Journal of Wildlife Management 75:1381-1398.

Schwab, A. C., and P. A. Zandbergen. 2011. Vehicle-related mortality and road crossing behavior of the Florida panther. Applied Geography 31:859-870.

South Dakota Game Fish and Parks. 2010. South Dakota mountain lion management plan. South Dakota Division of Wildlife, Pierre, South Dakota,USA.

Sunquist, M. E., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinios, USA.

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

Utah Division of Wildlife Resources. 1999. Utah cougar management plan. Utah Division of Wildlife Resources, Salt Lake City, Utah, USA.

Wilson, P. 1984. Puma predation on guanacos in Torres-del-paine National Park, Chile. Mammalia 48:515-522.

Wyoming Game and Fish Department. 2006. Wyoming mountain lion management plan. Wyoming Game and Fish Department, Lander, Wyoming, USA.

CHAPTER 2: COUGAR RESPONSE TO ROADS: THE INFLUENCE OF TRAFFIC, TOPOGRAPHY, AND LANDCOVER

INTRODUCTION

In North America roads have a profound effect on large carnivore management and conservation. For some carnivores, roads can act as barriers to movement and dispersal (Whittington et al. 2004, Dickson et al. 2005), reduce or degrade habitat (Mace et al. 1996, Mladenoff et al. 1999, Wielgus et al. 2002, Apps et al. 2004), and serve both directly (e.g., vehicle collisions) and indirectly (e.g., hunter and poacher access) as sources of mortality (Johnson et al. 2004, Nielsen et al. 2004, Nielsen et al. 2006, Ruth et al. 2011, Schwab and Zandbergen 2011). However, carnivore response to roads is highly complex and likely related to a combination of the adjacent landscape (e.g., landcover and topography) and traffic volume (Spellerberg 2002). Despite this, some studies examining carnivore-road relationships have not considered the surrounding landscape and almost none consider the associated road traffic (Northrup et al. 2012). Precluding either traffic or landscape when examining carnivore-road relationships could confound conclusions and ultimately lead to unnecessary or ineffective management actions aimed at mitigating non-existent effects.

For cougars (*Puma concolor*), the most widely distributed large carnivore in North America, metrics such as density of roads (km/km^2) and distance to nearest road have been used to examine home range establishment (Dickson and Beier 2002), selection of areas within a home range (Sweanor et al. 2008, Kertson et al. 2011), dispersal (Larue and Nielsen 2008), survival (Ruth et al. 2011) and areas of potential re-colonization (Belden and Hagedorn 1993, Thatcher et al. 2009, Larue and Nielsen 2011, LaRue et al. 2012). In addition, some researchers have considered road type (e.g., dirt or paved) in assessing cougar road crossings (Van Dyke et al. 1986, Cramer and Portier 2001, Dickson et al. 2005, Schwab and Zandbergen 2011). While some studies considered attributes of the landscape surrounding roads (Sweanor et al. 2008, Schwab and Zandbergen 2011), none considered information on traffic volume. Indeed, to date no study has examined how cougars react to roads in the context of adjacent landcover, topography and traffic.

As the growing human population demands more energy and space, road networks and their associated traffic will increase and inevitably encroach into occupied cougar habitats (Forman et al. 2003, Frair et al. 2008). Simultaneously, growing cougar populations are expanding and occupying portions of Midwestern North America, attracting the attention of both wildlife managers and the public (Larue and Nielsen 2011, LaRue et al. 2012). Considering these trends collectively, increasing our understanding of how cougars respond to roads and traffic will improve our ability to mitigate the effects of new roads in existing cougar habitats and predict potential areas of cougar re-colonization.

In this chapter I fit resource selection functions to GPS telemetry data from 12 cougars to examine how roads with different traffic volumes influence cougar selection of roadside landscapes. More specifically, my objective was to quantify how cougars alter their selection based on surrounding landcover and topography, and distance to roads based on traffic. I hypothesized that cougars would buffer themselves from roads with higher traffic volumes by selecting areas of either increased cover, greater ruggedness or farther from roads, than were available.

STUDY AREA

The study was conducted in the southwestern corner of Alberta, Canada near the town of Pincher Creek (49°29’ N, 113°57’ W; Fig.1). The 2600-km^2 area was bordered by Highway 3 to the north, the British Columbia-Alberta border to the west, the United States-Canada border to the south and Highway 6 to the east. The area was a mixture of private (35%) and public lands (65%). The private land, mainly located in the east, was characterized by flat rolling prairies intersected with deep-cut streams and rivers. Upland areas of private land were predominantly unforested grazing pastures interspersed with stands of aspen (*Populus tremuloides*) and willow (*Salix* spp.). The public land to the west was a mixture of foothills and rugged mountains, covered with Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*). The region is renowned for its strong winds ($\bar{x}$ = 19.8 km/hr) and climate characterized by warm ($\bar{x}$ = 26.2° C) dry ($\bar{x}$ = 32.5 cm/year) summers, and cold ($\bar{x}$ = -9.6° C) snowy ($\bar{x}$ = 328.9 cm/year) winters.

Human activities in the private lands were predominantly related to cattle ranching and recreational horseback riding. Human activities on public lands were year round service of oil and gas wells and intense summertime camping, angling, and off-road vehicle use.

The study area included 1,860 km of roads of which 255 km (~14%) were paved. Mean road density was 0.67 km/km^2 and paved road density was 0.16 km/km^2. The majority of roads had year round access with the exception of a few specific areas in the public lands.

METHODS

Cougar capture and GPS data

I used GPS telemetry data from 12 cougars (3-ad M, 2-sub-ad M, 5-ad F, 2-sub-ad F) captured during late winters (1 Jan - 15 Apr) of 2010 and 2011. Cougars were captured using trained hounds to track and tree them before administering 3 mg/kg Telazol® and 2 mg/kg Xylazine via remote injection (University of Alberta Animal Care Protocol #7191211 and Province of Alberta Collection and Research Permit #40819). I fitted cougars with Lotek 4400S GPS radiocollars (Lotek Engineering, Newmarket, ON, Canada), capable of remote download. Collars were programmed to acquire a GPS location every 3 hours. I attempted to locate and download GPS data biweekly for each cougar. After each download I identified clusters of ≥ 2 locations, within a 100-m radius within a 6 day time period using a time-space clustering algorithm from Knopff et al. (2009). Because landscape selection may be restricted during periods of feeding (Dickson et al. 2005, Knopff et al. 2009, Knopff 2011), and I was primarily interested in how cougars reacted to roads and traffic while active, I removed all locations identified as clusters and only included locations between clusters (i.e., when cougars were moving) in my analyses. Using the date and time at which each location was acquired, I designated locations as weekday day-time (Mon-Fri, sunrise-sunset), weekend day-time (Sat-Sun, sunrise-sunset) and night (sunset-sunrise) according to the monthly average time of sunrise and sunset for Pincher Creek, Alberta.

Road and traffic data

I obtained a single GIS layer which included the entire road network in the study area, as well as traffic volume for each segment (an un-intersected stretch of road), estimated as the number of vehicles per hour (vec/hr). Traffic volumes in the study area were estimated from a model incorporating counter data, trail cameras and additional landscape covariates (Northrup et al. 2012). Because traffic varies temporally, separate models and traffic volume predictions were created for weekday, weekend and night-time periods. A thorough description of the traffic model can be found in Northrup et al. (2012).

GIS data

From the road and traffic layer described above, I derived the average traffic volume per pixel (30m) using a 500-m radius moving window in ArcMap 10.0 (*traffic*). Using a moving window to calculate average traffic volumes effectively accounts for road density. Average traffic volume was calculated for each time period (weekday, weekend, night). Using the same resolution (pixel), I calculated the Euclidean distance from each pixel to the nearest road (*distance*). Using a digital elevation model (DEM) I calculated a terrain ruggedness index (*ruggedness*). Ruggedness is the sum change in elevation between a given pixel and the 8 pixels surrounding it (Riley et al. 1999). I reclassified a 30-m landcover map from the original 11 types into 2 types, open (agriculture, herbaceous, and burned) and forest (shrub, conifer and broadleaf forest). To aid in biological interpretation I binned traffic by 0.5 vehicles per hour, distance by 20 meters and ruggedness by 1 meter.

Cougar landscape selection

I used logistic regression to fit resource selection functions to cougar telemetry data (Johnson et al. 2006). Because previous studies concluded grizzly bears and wolves were unaffected by roads >500m distant (Mace et al. 1996, Rogala et al. 2011) I assumed cougars >500m from a road were likewise unaffected and thus only included cougar locations that fell within 500m of a road. Following a use-available design I generated 3 random locations for each used location within 500m of roads within each cougars 95% fixed kernel home range. I designated each random location as weekday, weekend or night in proportions equal to the observed proportions.

I developed a set of 6 *a priori* candidate models (Table 1) designed to evaluate if the inclusion of road and traffic data would better explain cougar landscape selection than data from the landscape alone. Because I suspected cougars might alter landscape selection with varying levels of traffic and distance to roads, I included several models with combinations of variable interactions. An interaction implies that cougar selection varies with changing values of the interacting variables. I checked for colinearity among predictor variables using the Pearson correlation coefficient. Highly correlated variables ($|r| \geq 0.7$) were not included in the same model. Because traffic volumes varied substantially between night and day (Northrup et al. 2012) I created 2 distinct data sets and fit separate models for day (weekday day-time and weekend day-time) and night.

To account for individual variation and unequal contribution to the overall sample, I fit candidate models using mixed-effects logistic regression with individual cougar as the random effect. I identified the best models using Akaike's Information Criterion adjusted for small sample sizes (AICc) and calculated AICc weights. I selected the model with the greatest AICc weight as the final model. Using estimated coefficients and standard errors from the final model, I calculated 95% confidence intervals for each regression coefficient and interpreted the magnitude of their effects as either "weak" where the 95% confidence interval spans zero or "strong" where the 95% confidence interval did not span zero. To evaluate which predictor variables and interactions had the greatest relative influence on selection, I calculated standardized beta coefficients following Menard (2004). Unless otherwise mentioned I used R 2.15.0 (Ihaka and Gentleman 1996) statistical software for all analyses.

RESULTS

Between April 2010 and December 2011 I obtained 13,660 successful GPS locations where cougars were designated as active (e.g., between clusters; $\bar{x}$ = 1,957 locations/cougar, SE = 257). Radiocollar fix success (# of successful fixes / # of attempted fixes) was 0.84 ($\bar{x}$ = 0.85 /cougar, SE = 0.006). Cougars were monitored for 102-628 days ($\bar{x}$ = 296 days/cougar, SE = 44.5). Of the active locations 6,409 (~47%) were located within 500m of a road, with 3,489 (55%) locations ($\bar{x}$ = 290 locations/cougar, SE = 40.5) labeled night, 2,068 (32%)

locations ($\bar{x}$ =173 locations/cougar, SE = 21.8) labeled weekday and 852 (13%) locations ($\bar{x}$ = 71 locations/cougar, SE = 11.4) labeled weekend. Night-time traffic ranged from 0.0-3.0 vec/hr with a mean of 0.73 vec/hr (SE = 0.004). Weekday day-time traffic range from 0.5-32.0 vec/hr with a mean of 4.21 vec/hr (SE = 0.07). Weekend day-time traffic ranged from 0.5-32.0 vec/hr with a mean of 4.23 vec/hr (SE = 0.06).

Day-time selection

The final model for day-time landscape selection had an AICc weight of 1.00 (Table 2.2A) and included data from distance to nearest road, traffic volume, terrain ruggedness, landcover type and several interactions between these covariates. Covariates with strong effects included *ruggedness*, *distance*, *landcover,* and the interaction of *ruggedness* × *distance*. All other variables had weak effects (Table 2.3A).

Ruggedness had the greatest relative influence on day-time selection, followed by *ruggedness* × *distance, distance, landcover*, *traffic* × *distance, traffic,* and *ruggedness* × *traffic* (Table 2.3A).

To aid interpreting the multiple interactions included in the final model, I created 3-dimensional plots with each combination of variable interactions plotted against the final predicted values and fit a 3rd order polynomial plane through the predicted values (Fig 2.2). I interpret these interactions by examining the general shape of the plane and relate it to the strength of its effect (e.g., strong vs. weak).

To distinguish the negative effect of open landcover types (Table 2.3A), I created separate plots for open and forested conditions. For each interaction the shape of the plane is consistent between landcover types but its relative position is lower under open conditions (Fig 2.2).

For the *traffic* × *distance* interaction, cougars selected for areas increasingly distant from roads of any traffic volume. The shape of the polynomial plane was generally flat as traffic volume increased, which reflects the weak effect of this interaction (Fig 2.2; Table 2.3A).

For the *ruggedness* × *distance* interaction, cougars selected areas of rugged terrain when close to roads, but this pattern decreased with increasing distance. In areas with little ruggedness, cougars selected distances farther from roads. The curved shape of the polynomial plane reflects the strong effect of this interaction (Fig 2.2; Table 2.3A).

For the *ruggedness* × *traffic* interaction, cougars selected for rugged terrain at all traffic volumes, but there was only a slight increase in selection for rugged terrain with increasing traffic. The shape of the polynomial plane was generally flat across increasing traffic volumes which reflects the weak effect of this interaction (Fig 2.2; Table 2.3A).

Night-time selection

The final model for night-time landscape selection was identical to the final day-time model with an AIC weight of 1.00 (Table 2.2B). This model included data from distance to nearest road, traffic volume, terrain ruggedness, landcover type and several interactions between these covariates. Covariates with strong effects included *ruggedness*, *distance*, *landcover*, and the 2-way interactions of *ruggedness* × *distance* and *ruggedness* × *traffic*. All other variables had weak effects (Table 2.3B). The *ruggedness* × *distance* interaction had the greatest relative influence on night-time selection, followed by *ruggedness*, *distance*, *ruggedness* × *traffic*, *landcover*, *traffic*, and *traffic* × *distance* (Table 2.3B).

Using the same procedure outlined for the final day-time model, I interpreted the multiple interactions included in the final night-time model by examining the shape of each polynomial plane and the strength of its effect (Fig 3; Table 2.3B). For the *traffic* × *distance* interaction, cougars selected for areas more distant from roads with greater traffic, but selection for roads with <1 vec/hr was virtually unaffected by distance. The shape of the polynomial plane was relatively flat across increasing traffic volumes which reflects the weak effect of this interaction (Fig 2.3; Table 2.3B).

For the *ruggedness* × *distance* interaction, cougars selected for areas of more rugged terrain at low distances from roads, but this pattern decreased with increasing distance. In areas with low ruggedness cougars selected for areas more distant from roads. The curved shape of the polynomial plane reflects the strong effect of this interaction (Fig 2.3; Table 2.3B).

For the *ruggedness* × *traffic* interaction, cougars selected for more rugged terrain with increasing traffic, but at low traffic volumes selection for rugged terrain was unaffected. The curved shape of the polynomial plane reflects the strong effect of this interaction (Fig 2.3; Table 2.3B).

DISCUSSION

Day-time selection

My results support the hypothesis that cougars will buffer themselves from roads and traffic by selecting areas with greater ruggedness, increased cover or being further from roads. During the day, cougars shielded themselves from roads of any traffic volume through a hierarchy of selection for rugged terrain, further distance from roads, and forest cover. Indeed, topography had the greatest influence on day-time selection suggesting the insulating effect of rugged terrain is greater than that of distance to road and landcover. Likewise, human disturbance has resulted in a similar pattern for elk in Yellowstone National Park where flight distances were shorter in the presence of rugged terrain, with elk first selecting ridges and then forest cover in response to cross-country skiers (Cassirer et al. 1992).

Interestingly, selection for rugged terrain declined as cougars were increasingly distant from roads, suggesting that cougars prefer lower levels of ruggedness but exceed this lower preference when close to roads. Although selection for rugged terrain has been relatively consistent among studies (Logan and Irwin 1985, Williams et al. 1995, Chetkiewicz and Boyce 2009), Dickson et al. (2005) found that cougars used areas of gentler terrain than their surroundings in Southern California. My study is the first to consider how selection for ruggedness can change with increasing distance from roads and thus potentially explain the apparent contradictions among previous studies. However, most previous studies differed in their quantification of terrain ruggedness and thus concluding similar or dissimilar patterns might be inappropriate.

In the absence of rugged terrain, cougars shielded themselves from roads by selecting areas farther from them. Florida panthers were found to use areas farther from recreational vehicle trails during periods of increased human use (e.g., ungulate hunting seasons; Janis and Clark 2002). Other researchers have concluded a similar displacement from areas around roads for caribou (Dyer et al. 2001), wolves (Whittington et al. 2004, Rogala et al. 2011), grizzly bears (Mace et al. 1996, Wielgus et al. 2002, Apps et al. 2004), and elk (Rowland et al. 2000) and most conclude the primary mechanism for displacement was human disturbance (i.e., traffic).

Results of my day-time selection analysis imply that if a road is surrounded by rugged terrain cougars will use areas close to that road irrespective of traffic. However, if the landscape surrounding a road is flat, cougars will select forested areas farther from roads, irrespective of traffic.

Night-time selection

At night cougars displayed a similar hierarchy of selection by buffering themselves from roads primarily through use of rugged terrain, and only in the absence of rugged terrain did they select areas farther from roads. However, the influence of the *traffic* × *ruggedness* interaction was greater at night, and cougar selection for increased ruggedness was apparent only when traffic exceeded ~1 vec/hr. Similarly, selection for areas more distant from roads was only apparent when traffic was >1 vec/hr. Indeed, at night cougars appeared ambivalent to roads with <1 vec/hr, suggesting that under the cover of darkness cougars are unaffected by roads with low levels of human use (i.e., traffic). Previous cougar research has documented night-time use of trails and gravel roads (Beier 1993, Dickson et al. 2005, Sweanor et al. 2008). Assuming these trails and gravel roads had a low level of human use at night, my results are consistent with these observations.

The influence of landcover was lower at night. Cougars still generally selected for forested areas, but the added cover of darkness appears to reduce the importance of forest cover. However, the steep increase in selection for rugged terrain with increasing traffic suggests that even with the increased cover of darkness cougars sought to isolate themselves from roads of greater traffic by selecting for increased ruggedness.

Overall, these results imply that cougars do not buffer themselves from roads receiving <1 vec/hr during night-time. If road traffic exceeds this level, cougars will attempt to insulate themselves by selecting areas of increased ruggedness. If rugged terrain is unavailable, cougars are likely to be farther from roads receiving >1 vec/hr.

Conclusions

The continued day-time use of roadside landscapes, despite shifting patterns of selection, combined with the night-time ambivalence towards roads receiving <1 vec/hr suggests that roadside habitats are at least somewhat attractive to cougars. Cougar attraction to roads has been previously documented (Dickson et al. 2005, Kertson et al. 2011) and is most likely related to prey distribution and abundance. White-tailed and mule deer were the prey most commonly killed by cougars in my study area (J. E. Banfield 2010, unpublished data), and both of these deer species have been documented using roadside habitats (Muhly et al. 2011). My results suggest that cougars may recognize the higher abundance of prey in the vicinity of roads and capitalize on this during periods of decreased human use (e.g., night-time).

My conclusion that roads may force cougars to use more rugged terrain than they normally would in absence of roads could have implications for cougar-prey relationships. For example, although rugged terrain is generally thought to enable prey capture (Logan and Irwin 1985, Koehler and Hornocker 1991), beyond some optimum level terrain ruggedness might reduce a cougar's ability to detect prey. Future studies of cougar-road relationships should consider the impact of roads on specific life requirements such as predation.

MANAGEMENT IMPLICATIONS

My results imply that a cougar's response to roads depends more on the landscape surrounding a road and less on the associated traffic. In areas with existing cougar populations, managers responsible for cougar conservation are urged to consider roadside topography when assessing the potential impacts of expanding road networks. Similarly, individuals living near the wildland-urban interface (Kertson et al. 2011), should be aware that nearby rugged terrain can provide cougars with a false sense of security that could result in an increased probability of human-cougar encounters. Managers aware of areas with an increased probability of encounters should provide residents with educational materials on cougar aggression and the appropriate human response (Sweanor et al. 2008).

Future models aimed at predicting areas of cougar expansion and re-colonization should incorporate the insulating effects of roadside topography. Finally, despite our current understanding of cougar-road relationships, managers should be cognizant of the cougar’s potential for behavioural plasticity (Kertson et al. 2011, Knopff 2011), and should employ an adaptive approach to cougar management and conservation (Cougar Management Guidelines Working Group 2005).

Table 2. 1. Model structure of 6 a priori candidate models used to examine roadside landscape selection for 12 cougars in southwestern Alberta, Canada.

Model	Model Structure
1	*landcover + ruggedness*
2	*landcover + ruggedness + distance*
3	*landcover + ruggedness + distance + traffic*
4	*landcover + ruggedness + distance + traffic + (traffic × distance)*
5	*landcover + ruggedness + distance + traffic + (traffic × distance) + (ruggedness × distance)*
6	*landcover + ruggedness + distance + traffic + (traffic × distance) + (ruggedness × distance) + (ruggedness × traffic)*

Table 2. 2. Day-time (A) and night-time (B) model selection for resource selection functions fit to 12 cougars in southwestern Alberta, Canada.

A)

Model covariates	ΔAICc	*w*	*K*	Rank
landcover + ruggedness + distance + traffic + (traffic × distance) +(ruggedness × distance)+ (ruggedness × traffic)	0.00	>0.99	9	1
landcover + ruggedness + distance	37.8	0.00	5	2
landcover + ruggedness + distance + traffic	39.3	0.00	6	3
landcover + ruggedness + distance + traffic + (traffic × distance) + (ruggedness × traffic)	39.5	0.00	8	4
landcover + ruggedness + distance + traffic + (traffic × distance)	39.9	0.00	7	5
landcover + ruggedness	69.8	0.00	4	6

B)

Model covariates	ΔAICc	*w*	*K*	Rank
landcover + ruggedness + distance + traffic + (traffic × distance) +(ruggedness × distance)+ (ruggedness × traffic)	0.00	>0.99	9	1
landcover + ruggedness + distance + traffic + (traffic × distance) + (ruggedness × traffic)	36.4	0.00	8	2
landcover + ruggedness + distance + traffic + (traffic × distance)	43.1	0.00	7	3
landcover + ruggedness	47.4	0.00	4	4
landcover + ruggedness + distance + traffic	47.5	0.00	6	5
landcover + ruggedness + distance	48.2	0.00	5	6

Table 2. 3. Day-time (A) and night-time (B) selection coefficients (β) and 95% confidence intervals for final model covariates used to assess cougar response to roads in southwestern Alberta, Canada. Standardized beta coefficients are reported (Std. β**)**.

A)

Covariate	**β**	**SE**	**95% CI**		**Std. β**
			Lower	**Upper**	
Ruggedness	0.053	0.005	0.04	0.06	0.560
Distance	0.054	0.006	0.04	0.06	0.377
Traffic	0.005	0.008	-0.01	0.02	0.029
Landopen	-0.453	0.049	-0.55	-0.36	-0.217
traffic × *distance*	-0.001	<0.000	-0.01	<0.00	-0.065
ruggedness × *distance*	-0.002	<0.000	<-0.00	<-0.00	-0.388
ruggedness × *traffic*	0.001	<0.000	<-0.00	<0.00	0.026

B)

Covariate	**β**	**SE**	**95% CI**		**Std. β**
			Lower	**Upper**	
Ruggedness	0.030	0.005	0.02	0.04	0.315
Distance	0.024	0.007	0.01	0.04	0.166
Traffic	-0.138	0.085	-0.30	0.03	-0.068
Landopen	-0.151	0.043	-0.24	-0.07	-0.072
traffic × *distance*	0.006	0.006	-0.01	0.02	0.047
ruggedness × *distance*	-0.002	<0.000	<-0.00	<-0.00	-0.316
ruggedness × *traffic*	0.013	0.004	0.00	0.02	0.125

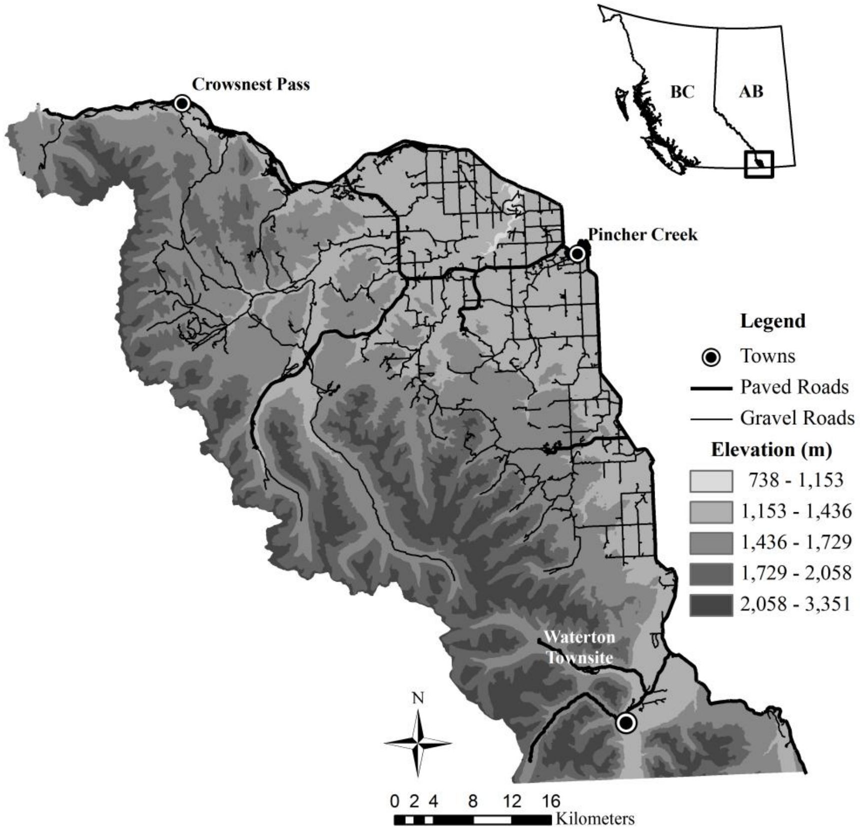

Figure 2. 1. Map of the study area in southwestern Alberta, Canada.

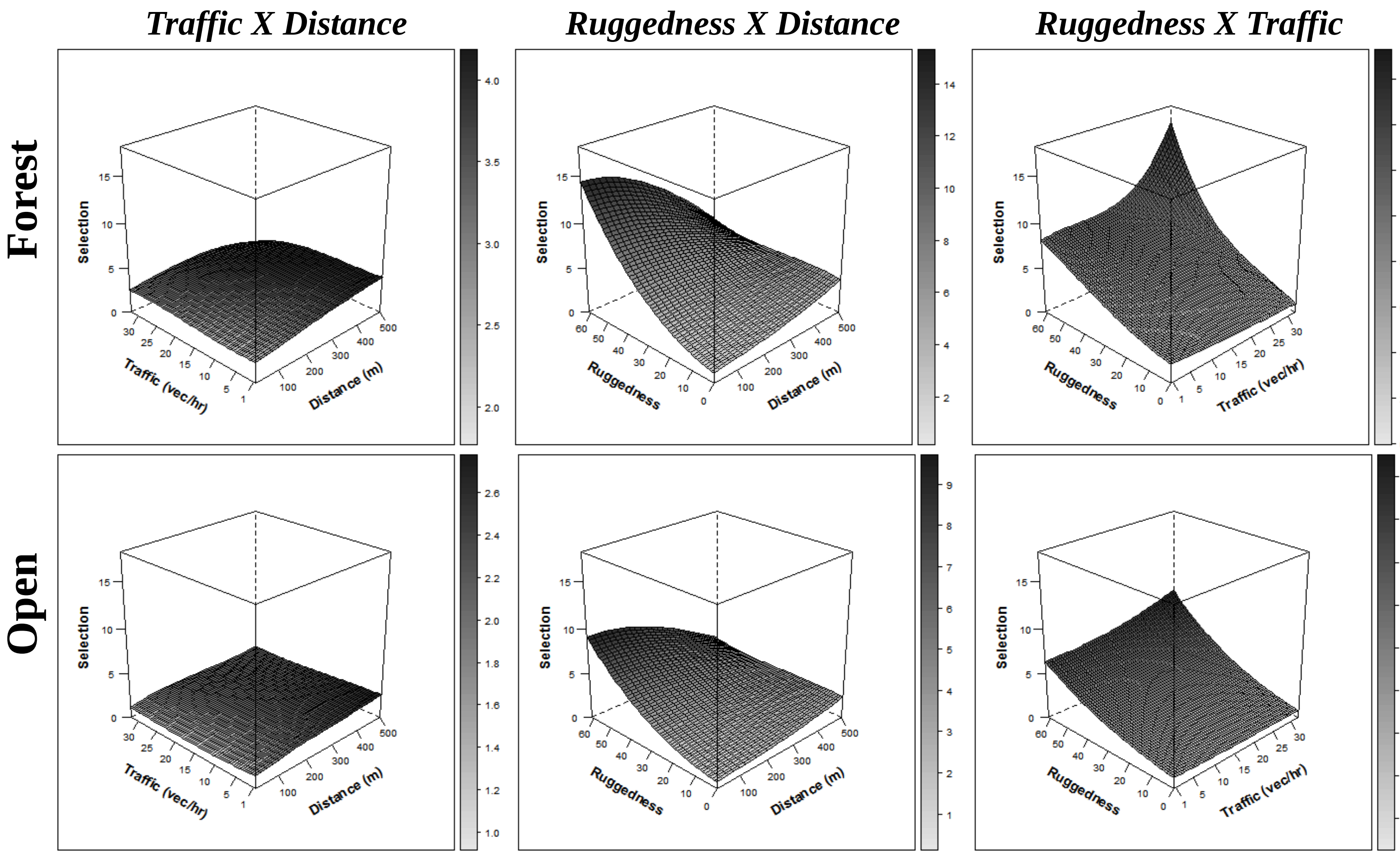

Figure 2. 2. Third-order polynomial surfaces fit to probability of day-time landscape selection against each combination of variable interactions for the top day-time landscape selection model.

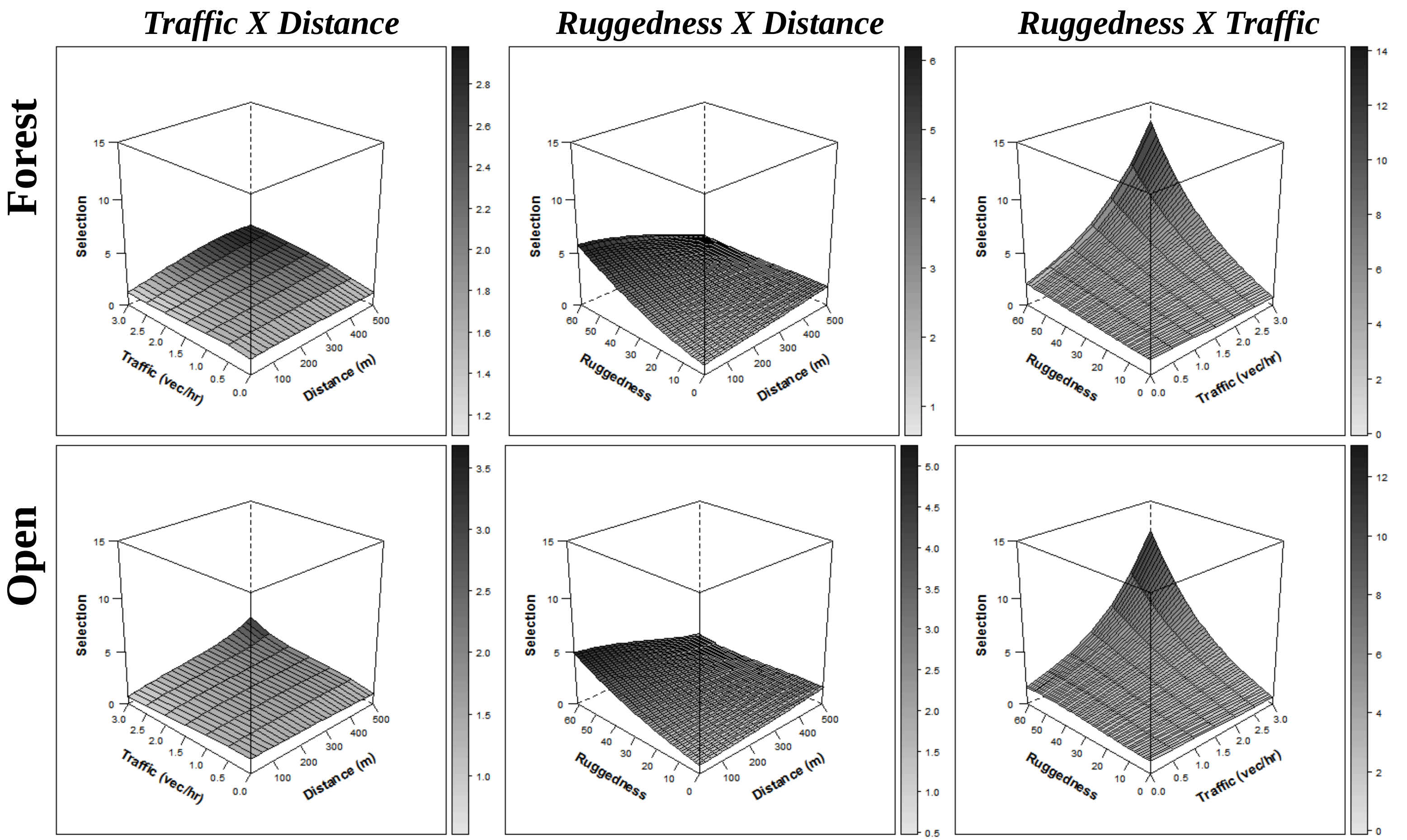

Figure 2. 3. Third-order polynomial curves fit to probability of night-time landscape selection against each combination of variable interactions for the top night-time landscape selection model.

LITERATURE CITED

Apps, C. D., B. N. McLellan, J. G. Woods, M. F. Proctor, and S. Gehrt. 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. Journal of Wildlife Management 68:138-152.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94-108.

Belden, R. C., and B. W. Hagedorn. 1993. Feasibility of translocating panthers into northern Florida. Journal of Wildlife Management 57:388-397.

Cassirer, E. F., D. J. Freddy, and E. D. Ables. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. Wildlife Society Bulletin 20:375-381.

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

Cougar Management Guidelines Working Group. 2005. Cougar managment guidelines. WildFutures, Bainbridge, WA, USA.

Cramer, P. C., and K. M. Portier. 2001. Modeling Florida panther movements in response to human attributes of the landscape and ecological settings. Ecological Modelling 140:51-80.

Dickson, B. G., and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. Journal of Wildlife Management 66:1235-1245.

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.

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of Industrial Development by Woodland Caribou. Journal of Wildlife Management 65:531-542.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Farig, R. France, C. Goldman, K. Heanue, J. Jones, F. Swanson, T. Turrentine, and T. Winter. 2003. Road Ecology: Science And Solutions. Island Press, Washington DC.

Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. Journal of Applied Ecology 45:1504-1513.

Janis, M. W., and J. D. Clark. 2002. Responses of Florida panthers to recreational deer and hog hunting. Journal of Wildlife Management 66:839-848.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: Application of the Andersen-Gill model to Yellowstone grizzly bears. Journal of Wildlife Management 68:966-978.

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.

Kertson, B. N., R. D. Spencer, J. M. Marzluff, J. Hepinstall-Cymerman, and C. E. Grue. 2011. Cougar space use and movements in the wildland-urban landscape of western Washington. Ecological Applications 21:2866-2881.

Knopff, A. A. 2011. Conserving cougars in a rural landscape: Habitat requirements and local tolerance in west-central Alberta. University of Alberta, Edmonton, Alberta, Canada.

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.

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

Larue, M. A., and C. K. Nielsen. 2008. Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. Ecological Modelling 212:372-381.

_____. 2011. Modelling potential habitat for cougars in midwestern North America. Ecological Modelling 222:897-900.

LaRue, M. A., C. K. Nielsen, M. Dowling, K. Miller, B. Wilson, H. Shaw, and C. R. Anderson. 2012. Cougars are recolonizing the midwest: Analysis of cougar confirmations during 1990–2008. Journal of Wildlife Management in press.

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

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.

Menard, S. 2004. Six approaches to calculating standardized logistic regression coefficients. American Statistician 58:218-223.

Mladenoff, D. J., T. A. Sickley, and A. P. Wydeven. 1999. Predicting gray wolf landscape recolonization: Logistic regression models vs. new field data. Ecological Applications 9:37-44.

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.

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.

Northrup, J., J. Pitt, T. Muhley, B, 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 in press.

Riley, S. J., S. D. DeGloria, and R. Elliott. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23-27.

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 16:16.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672-684.

Ruth, T. K., M. A. Haroldson, K. M. Murphy, P. C. Buotte, M. G. Hornocker, and H. B. Quigley. 2011. Cougar survival and source-sink structure on greater Yellowstone's northern range. Journal of Wildlife Management 75:1381-1398.

Schwab, A. C., and P. A. Zandbergen. 2011. Vehicle-related mortality and road crossing behavior of the Florida panther. Applied Geography 31:859-870.

Spellerberg, I. F. 2002. Ecological effects of roads. Science Publishers, Inc., Enfield, New Hampshire, USA.

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

Thatcher, C. A., F. T. van Manen, and J. D. Clark. 2009. A habitat assessment for Florida panther population expansion into central Florida. Journal of Mammalogy 90:918-925.

Van Dyke, F. G., R. H. Brocke, and H. G. Shaw. 1986. Use of road track counts as indexes of mountain lion presence. Journal of Wildlife Management 50:102-109.

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 9:4.

Wielgus, R. B., P. R. Vernier, and T. Schivatcheva. 2002. Grizzly bear use of open, closed, and restricted forestry roads. Canadian Journal of Forest Research 32:1597.

Williams, J., S, J. McCarthy, J, and H. Picton, D. 1995. Cougar habitat use and food habits on the Montana rocky mountain front. Intermountain Journal of Sciences 1:16-28.

CHAPTER 3: COUGAR PREDATION BEHAVIOUR: DO COUGARS AMBUSH OR STALK THEIR PREY?

INTRODUCTION

Predatory behaviour of large carnivores is an essential component of their ecology and management (Knopff et al. 2009). Differential predatory behaviours such as whether a carnivore employs a coursing (actively chasing) or ambush (sit and wait) strategy influences prey selection patterns (Kunkel et al. 1999, Pierce et al. 2000, Husseman et al. 2003, Knopff 2010) and has been suggested as a determinant of whether predation is additive or compensatory (Wilmers et al. 2007). Predatory behaviour could also have implications for estimates of kill rate (Knopff et al. 2010, Ruth et al. 2010) or parameterization of functional response models (Holling 1959). For example, recent studies have used GPS-based animal movement data to distinguish between two central components of the functional response (Holling 1959, Merrill et al. 2011), handling time (time required to consume prey) and search time (time required to locate, capture and kill prey; Zimmermann et al. 2007, Sand et al. 2008, Knopff et al. 2009, Merrill et al. 2011, McPhee et al. 2012). With GPS data, the distinction between handling time and search time generally begins by identifying periods of movement, where consecutive GPS locations are spatially distant above some predetermined level, and clusters, where numerous GPS locations are centered in a relatively small spatial area. Field crews then visit clusters labeling them as kill sites based on the presence of prey remains. Once clusters have been identified as kill sites, the locations at or near kills are allocated to handling time while the locations moving between kills are allocated to search time (Merrill et al. 2011). In this simple dichotomy, the kill itself represents the end of search time and the start of handling time, and is implicitly assumed to occur at or near the movement-cluster boundary (i.e., where the animal transitions from movement to non-movement). While this assumption may be reasonable for an active (coursing) predator; for an ambush predator, some beginning portion of time at a kill cluster might actually be time spent waiting (searching) for prey, confounding the distinction of handling time. Handling time directly affects the shape of the functional response and at high prey densities it determines the point at which the function asymptotes (McKenzie et al. 2009, McKenzie et al. 2012). Incorrectly allocating GPS locations to handling time leads to an underestimation of kill rate (number of prey killed per predator per unit time). Determining whether a carnivore employs an ambush or active style of predation, which affects the distinction between handling time and search time, could support implicit assumptions and increase confidence in parameterization of functional response models.

Despite this, ambiguity regarding predatory behaviour still exists for some large carnivores in North America. Cougars (*Puma concolor*), for example, have been labeled ambush predators by some (Husseman et al. 2003, Rominger et al. 2004, Wilmers et al. 2007, Krumm et al. 2010) and stalking (active) predators by others (Young and Goldman 1946, Kunkel et al. 1999, Pierce et al. 2000, Knopff 2010). Rare observations of cougar-prey interactions suggest they are predominantly stalking predators, with most accounts describing cougars using terrain, vegetation and stasis to gradually reduce the distance to prey before initiating an attack (Koford 1946, Young and Goldman 1946, Robinette et al. 1959, Wilson 1984, Bank and Franklin 1998). Similar descriptions of cougar predatory behaviour have been inferred from snow-tracking (Hornocker 1970, Laundre and Hernandez 2003). However, establishing a carnivore's dominant predatory strategy should include a quantitative assessment of repeated observations on unique individuals in a manner free of observer bias.

Currently, only one researcher has published this type of study for cougar predation behaviours (Beier et al. 1995). Using intensive night-time radio tracking, Beier et al. (1995) attempted to distinguish cougar behaviours (including predation) from movement patterns and thus describe "how cougars hunt". However, this study primarily examined cougar distance travelled per night and did not report on the distinct movements made prior to the kill itself. Indeed, without a precise estimate of when a kill occurred combined with the movements leading to that kill, concluding which strategy the cougar used to accomplish the kill remains problematic.

GPS radiocollars capable of short fix intervals and equipped with dual-axis activity sensors offer a promising approach to quantifying cougar predation behaviours. Animal behaviours can be inferred from changes in movement metrics such as step length (straight line distance between 2 consecutive relocations; Turchin 1998) and turn angle (the angle between the direction of the current movement and the previous; Fryxell et al. 2008, Van Moorter et al. 2010). Activity-sensor data varies with collar manufacturer but is generally designed to be a measure of head movement (Lotek Engineering, Newmarket, ON, Canada).

Over the past decade, several manufacturers have equipped GPS collars with dual-axis motion sensors capable of recording side-to-side movements (*x*) and forward-and-backward movements (*y*). Combining fine-scale GPS location data with simultaneously recorded activity data could provide detailed information (Loettker et al. 2009) necessary to test specific hypotheses regarding the dominant predatory strategy employed by cougars.

In this chapter, I used GPS location data with a 15-minute fix interval, collar activity data recorded at a 64-second interval, and data collected during field visits to GPS clusters to assess cougar predation behaviour. My objective was to infer the cougar's dominant predatory strategy, either stalking (active) or ambush (sit and wait), from movements and activity data leading up to the movement-cluster boundary. To distinguish behaviours associated with cougar predation, I contrasted step lengths and activity data between movements leading to a field-validated kill cluster (where prey remains were present) and movements leading to a field-validated non-kill cluster (where prey remains were absent). If cougars are primarily stalking predators I expected to see differences in step lengths and activity data between kill movements and non-kill movements at some point near the movement-cluster boundary. Differences in these metrics would suggest the kill occurred prior to cluster formation indicating the cougar was actively searching for prey while moving about the landscape and not waiting in ambush. Conversely, if cougars are ambush predators I expected no differences in step length and activity data between kill and non-kill movements. No difference in metrics would suggest the kill did not occur prior to cluster formation and therefore must have occurred at some time within the cluster, indicating the cougar moved into the kill cluster and laid in ambush for prey to wander by. Specifically, I hypothesized that relative to kill movements, at some interval approaching the movement-cluster boundary, step lengths would be shorter, reflecting slow movements associated with a stalk (Wilson 1984, Beier et al. 1995). Minimum activity also would be lower, because cougars have been observed using stasis when approaching prey (Robinette et al. 1959, Wilson 1984, Bank and Franklin 1998), and finally maximum activity would be greater, reflecting the sudden lunge of an attack and potentially an ensuing struggle with the prey (Young and Goldman 1946, Robinette et al. 1959).

A secondary but related hypothesis could make predictions regarding the activity data within (after the cluster began) kill and non-kill clusters. If cougars were stalking predators I expected the initial activity data to be significantly greater in kill clusters than in non-kill clusters, indicative of feeding behaviours and owing to the likelihood that the prey already has been killed. Conversely, if cougars are ambush predators I expected activity data within kill clusters to be initially similar to non-kill clusters reflecting a cougar laying in ambush, but ultimately followed by a sudden increase at some point (i.e., initiation of the attack) after the start of the cluster.

STUDY AREA

The study took place near the town of Pincher Creek in southwestern Alberta, Canada (49°29’ N, 113°57’ W; Fig.1). The landscape was contrasted by a sharp transition from flat prairies in the east abruptly rising to rugged mountains in the west. The area was a mixture of private (35%) and public lands (65%). The private land, located in the eastern half of the study area, was mostly un-forested grazing pastures interspersed with upland stands of willow (*Salix* spp.), and aspen (*Populus tremuloides*). The public land to the west was predominantly forested with Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*). The climate was characterized by strong winds ($\bar{x}$ = 19.8 km/hour), warm ($\bar{x}$ = 26.2° C) dry ($\bar{x}$ = 32.5 cm/year) summers and cold ($\bar{x}$ = -9.6° C) snowy ($\bar{x}$ = 328.9 cm/year) winters. Human presence on private lands was predominantly related to cattle ranching. Human presence on public lands was predominantly recreational with intense use of off-road vehicles in summer and snowmobiles in winter. Service of oil and gas wells was active year round.

The main prey available to cougars during the study were white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), moose (*Alces alces*), elk (*Cervus elaphus*), and beaver (*Castor canadensis*). Bighorn sheep (*Ovis canadensis*) and mountain goat (*Oreamnos americanus*) were found in small groups at high elevations. Other carnivores present in the area included grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolves (*Canis lupis*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), and red fox (*Vulpes vulpes*).

METHODS

Cougar capture and collaring

I used data from 10 cougars (2-ad M, 1-sub-ad M, 5-ad F, 2-sub-ad F) captured during late winters (1 Jan – 15 Apr) of 2010 and 2011. I captured cougars using trained hounds to track and tree them before administering 3 mg/kg Telazol® and 2 mg/kg Xylazine via remote injection (University of Alberta Animal Care Protocol #7191211 and Province of Alberta Collection and Research Permit #40819). I fitted cougars with Lotek 4400S GPS radiocollars (Lotek Engineering, Newmarket, ON, Canada), capable of remote download and equipped with dual-axis activity sensors.

GPS data

Upon deployment, collars were programmed to acquire a GPS location every 3 hours. To collect locations at a finer temporal scale I periodically changed collar fix schedules to 15-minute intervals for periods of 10-23 days via remote upload. I collected 15-minute fix data for each cougar, for at least 10 days in both summer (16 Apr – 15 Nov) and winter (16 Nov – 15 Apr) seasons. At the conclusion of each 15-minute monitoring period, collars would automatically return to a 3-hour fix interval. I attempted to download GPS locations at the midpoint and end of each 15-minute monitoring period.

After each download I identified clusters of ≥2 locations, within a 50m radius within a 6 day time frame using a time-space clustering algorithm from Knopff et al. (2009). The clustering algorithm calculates the geometric center of each cluster, which I then input into a handheld GPS to locate and visit clusters in the field. Following Knopff et al. (2009), I designated the cluster as a kill cluster if I found the presence of prey remains or evidence of cougar feeding behaviours. If prey remains were found, I recorded the species, age and sex of the prey. Clusters where no prey remains were found were designated as non-kill clusters.

Using a GIS, I connected consecutive 15-minute locations with straight lines (hereafter called steps; Turchin 1998). If the number of steps between two clusters was >6 I truncated it to the 6 consecutive steps immediately preceding the cluster, encompassing data collected during the 90 minutes prior to a cluster. I designated these sets of ≤6 steps as *kill paths* if they lead to a kill cluster and *non-kill paths* if they lead to a non-kill cluster, and collectively refer to them as *pre-cluster paths*. Similarly, if a cluster contained >6 steps I truncated it to the initial 6 consecutive steps encompassing data collected during the first 90 minutes within a cluster. I truncated pre-cluster paths to only 6 steps because it was nearly equal to the mean number of steps (6.3, SE = 2.6) traveled between any 2 clusters. I truncated clusters to only the first 6 within-cluster steps because 1) Beier et al. (1995) speculated that prey were killed within 60 minutes of a cougar arriving at a kill site, and 2) for symmetry with the number of pre-cluster steps. I categorized each step according to the time it occurred relative to the start of the cluster (time 0); with pre-cluster steps assigned a negative time and within cluster steps assigned a positive time (Fig. 2). In other words, steps that occurred prior to the cluster start were labeled -90,-75…-15, and steps occurring after the cluster start were labeled +15, +30…+90.

Collar activity data

Upon deployment, radiocollars were programmed to record activity data every 64 seconds. Activity data included the date and time of the interval as well as an ‘x’ value, determined by the number of times the collar breaks the x-axis (side to side movement), and a ‘y’ value, determined by the number of times the collar breaks the y-axis (forward and backward movement) in the preceding 64-second interval. I retrieved collar activity data directly from each collar after removal from the cougar. I summed x and y activity values and joined each line of data to its corresponding step based on the time stamp. Because activity data were recorded at 64-second intervals each step was joined with a set of ~14 lines of activity data.

Statistical analyses

For each step I calculated step length as the straight-line distance between consecutive telemetry relocations, and from the corresponding set of activity data I selected the maximum and minimum values. To test my hypotheses related to movements prior to a cluster event, I used mixed-effects logistic regression, with individual cougars as the random effect, to examine differences in step length and maximum and minimum activity values between kill and non-kill paths within each time interval.

Because landscape heterogeneity and human activities can affect cougar movements (Dickson et al. 2005) potentially causing variation in step lengths and activity data, I tested for differences in habitat use along kill and non-kill paths. Using a GIS I reclassified a 30-m landcover map from the original 11 categories into 2 landcover types, forest and open. I calculated the proportion of forest along each step as the length of the step within forest cover divided by the total length of the step. I used a 30-m digital elevation model (DEM) to calculate an index of terrain ruggedness and the degree of slope (Riley et al. 1999). Using a road layer (vector) provided by Alberta Sustainable Resource Development I created a 30-m distance from roads (raster) map. For each pre-cluster step I calculated the length-weighted mean of the terrain ruggedness, degree of slope, and distance to nearest road. The length-weighted mean was calculated by dividing each step into segments that pass through a single pixel. The length of each segment is then multiplied by the value of the pixel, summed across the entire step, and then divided by the total step length. I used mixed-effects logistic regression, with individual cougar as the random effect to contrast these habitat and human-related variables between kill and non-kill paths within each time interval. If coefficient *P*-values were >0.05, I concluded the habitat characteristics between kill and non-kill paths at that time were similar and did not significantly affect step lengths or activity values.

To test my hypotheses related to within-cluster activity, I used mixed-effects logistic regression, with individual cougar as the random effect, to examine differences in maximum and minimum activity values between kill and non-kill clusters within each time interval.

To account for seasonal differences in snow accumulation and foliage, I conducted separate analyses for winter and summer seasons. Unless stated otherwise I used R 2.15.0 (R Development Core Team 2008) for all analyses.

RESULTS

From May 2010 to June 2011 I collected 44,251 15-minute GPS locations spread over 431 cougar days, with a mean of 43.1 (SE = 3.98) days/cougar (Fig. 3). I visited 553 GPS clusters identifying 53 (summer = 27) kills and 459 (summer = 220) non-kills. All cougar killed prey were ungulates including deer

(81%), moose (9%), elk (8%), and mountain goat (2%). In autumn 2011, I retrieved all collars and collected >1,000,000 rows of activity data.

Pre-cluster analyses

Winter kill-path step lengths at -30 and -15 minutes were significantly shorter than non-kill paths ($P < 0.05$; Fig. 4). Summer-season step lengths were similar for all times between kill and non-kill paths ($P > 0.05$).

Winter-season maximum activity values were similar for all pre-cluster times ($P > 0.05$) except -15 minutes. Winter-season maximum activity obtained during -15 minutes was greater in kill paths over non-kill paths ($P < 0.05$). Summer trends were identical with maximum activity being similar at all times except -15 minutes where kill path values were greater than non-kill paths ($P < 0.05$; Fig. 4).

Summer-season minimum activity values were similar for all pre-cluster times ($P > 0.05$). Winter-season minimum activity values were similar for all pre-cluster times ($P > 0.05$), except -30 minutes where minimum activity was lower for kill paths ($P < 0.05$; Fig. 4).

Winter-season habitat use was similar at all pre-cluster times between kill paths and non-kill paths ($P > 0.05$). Summer-season habitat use was similar for all pre-cluster times ($P > 0.05$) except -30 and -15 minutes. Proportion of forest was lower for kill path steps at -30 and -15 minutes ($P < 0.05$). All other summer variables at these times were similar ($P > 0.05$; Table 1).

Within-cluster analyses

Maximum activity values within kill clusters were higher than non-kill clusters at all times ($P < 0.05$) in both seasons. Similarly, minimum activity values within kill clusters were higher than non-kill clusters at all times ($P < 0.05$; Fig. 4) and seasons.

DISCUSSION

Pre-cluster analyses

The results of my pre-cluster analyses support the hypothesis that cougars are primarily stalking predators. Similarities in winter-season step lengths between kill and non-kill paths from times -90 through -45 imply that during this period cougars were still searching for prey. Shorter step lengths along pre-kill paths beginning at -30 minutes and continuing through -15 minutes suggest a transition to stalking behaviour and support the prediction that cougars slowly stalk their prey (Wilson 1984, Beier et al. 1995, Bank and Franklin 1998) with shorter pre-kill cluster movements.

The lack of differences in winter habitat use between kill and non-kill paths suggests the changes in winter step lengths were related to behavioural changes resulting from cougars locating, stalking and killing prey. Although unrelated to my primary objective, this also suggests that cougars use similar winter habitats during each phase of predation (i.e. searching, stalking, killing). Previous studies have assumed that cougars will use habitats that would allow them to seize any opportunity to make a kill (Holmes and Laundre 2006). My results support this assumption and infer that the winter habitats cougars use to locate prey are similar to the habitats used to stalk and kill prey.

Summer season step lengths between kill and non-kill paths did not reveal a pattern identical to the winter season, however, I concluded a similar trend from shorter mean step lengths and a nearly significant *P*-value at -15 minutes ($P = 0.06$). One plausible explanation for the discrepancies between seasons could be related to differences in vegetation. Intuitively, summertime vegetation increases the amount of low-level cover, which may result in an increased rate at which cougars can stalk prey while remaining undetected (Robinette et al. 1959). This explanation is further substantiated by the results of my summer season habitat analyses, where the proportion of forest cover at -30 and -15 minutes was significantly lower along kill paths (Table 1). This indicates that in the 30 minutes prior a kill cluster, cougars used more herbaceous or shrub type habitats to approach and kill prey.

The use of more open habitats in summer, considered collectively with shorter step lengths in winter at kill path times -30 and -15 point to a seasonal trade off in how cougars stalk their prey. In winter, a lack of low level cover might require cougars to use stasis and slower movements to remain undetected when stalking prey. This does not imply that cougars avoid wintertime cover, only that slower movement might be necessary to remain undetected when low level cover is rare. In summer, low-level herbaceous vegetation growing in un-forested areas might allow cougars to more rapidly approach prey in more open areas while remaining undetected. Robinette et al. (1959) reported a summer-time observation of a cougar using low brush to approach a group of deer to within 3m in just a few minutes. Bothma and LeRiche (1984) found vegetation as short as 200cm could conceal hunting leopards (*Panthera pardus*). Assuming cougars could similarly use short vegetation for effective concealment, herbaceous and shrub type habitats would be ideal for rapid summer season stalks.

The increase in maximum activity for kill paths at -15 minutes further supports the hypothesis that cougars are stalking predators. Consistency in patterns of maximum activity across seasons, suggests the differences in the summer time habitat use had little influence on this metric. I interpret the sudden increase in activity at -15 minutes as being directly related to the cougar attacking prey. Indeed, observational accounts describe cougars making several quick bounds before contacting prey followed by a short struggle (Robinette et al. 1959, Bank and Franklin 1998).

The general lack of differences in minimum activity conflicts with the previous metrics supporting the stalking-predation hypothesis. Minimum activity was significantly different only at -30 minutes in winter, where the value was lower for kill paths. While this difference was in the direction predicted for a stalking predator, the lack of significant differences at the following time (-15), combined with the lack of differences at all times in summer make it difficult to interpret this metric. Wilson (1984) described cougar movements when hunting as repeated periods of stasis where the cougar “sat and watched.” If cougars regularly remain still or move little while searching for prey (Beier et al. 1995), then using this metric to distinguish between searching and stalking behaviours would be difficult.

Within-cluster analyses

The results of my within-cluster analyses support the hypothesis that cougars are stalking predators. Both maximum and minimum activity values were significantly greater in kill clusters over non-kill clusters. If cougars were ambush predators the expectation was that initial activity values would be similar between kill and non-kill clusters, suggesting that cougars were waiting in ambush for prey to wander by. I interpret the pattern of higher activity in kill clusters as being related to the head movements associated with feeding behaviours, which implies the kill was already completed at the time the cluster began.

Predatory behaviour

Although I was unable to support every prediction related to the stalking hypothesis, clear results from my within-cluster analyses combined with the patterns in maximum activity suggest that cougars are primarily stalking predators. Changes in winter kill path step lengths at times near the movement-cluster boundary also support this and inconsistencies in summer step lengths can be explained by differences in summer habitat use along kill paths. Despite contradictions from minimum activity values, all other metrics support my original predictions and provide sufficient evidence to conclude that cougars are primarily stalking predators.

Conclusions

My results conflict with the common assertion that cougars are less selective than coursing predators when choosing prey (Wilmers et al. 2007). While this assumption may seem logical for an ambush predator, a mobile stalking predator should not be expected to be any less selective than a coursing predator. Indeed, the majority of studies initially hypothesizing differences in prey selection between cougars and canids (Kunkel et al. 1999, Pierce et al. 2000, Husseman et al. 2003), ultimately concluded cougars were similarly as selective as both wolves (Kunkel et al. 1999) and coyotes (Pierce et al. 2000). More recent studies of cougar prey selection also have concluded that cougars select for vulnerable prey with regard to age and reproductive status (Knopff et al. 2010) or disease (Krumm et al. 2010). Given the risks associated with attacking prey (Ross et al. 1995, Logan and Sweanor 2001) an active predator capable of observing, stalking and attacking specific individuals should select for vulnerable prey (Knopff 2010). When estimating cougar kill rate or functional response most authors allocate GPS-telemetry relocations at kills to handling time and locations between kills to search time (Anderson and Lindzey 2003, Mattson 2007, Knopff et al. 2009, Ruth et al. 2010). In doing so the kill is assumed to occur during the interval preceding a kill cluster (Anderson and Lindzey 2003, Mattson 2007, Knopff et al. 2009, Ruth et al. 2010) suggesting an active style of predation. My results support this assumption and add confidence to pre-existing estimates of cougar kill rates. Indeed, the increase in maximum activity during the interval immediately preceding a kill cluster (-15) combined with the activity within-kill-clusters suggests the kill did in fact occur prior the cluster and that during the beginning intervals of the kill cluster, the prey was already dead. While my results are based on GPS locations collected at a 15-minute fix interval, assumptions of when the kill occurred should remain reasonable at nearly any fix interval.

MANAGEMENT IMPLICATIONS

In this chapter I present the first evaluation of fine-scale GPS data, collar activity data, and field-validated kill sites to quantify cougar predation behaviours. Patterns of cougar activity in this study suggest that cougars are active predators, moving through the landscape to locate, stalk and kill prey. Wildlife managers should consider the ability of cougars to select vulnerable prey when assessing or modeling ungulate population dynamics (but see Husseman et al. 2003). For managers modeling cougar kill rate or functional response, my results support the assumption that cougars kill prey in the interval preceding a kill cluster and therefore the common procedure of using kill clusters to distinguish handling time from search time is justified.

Table 3. 1. Summary of logistic regression tests for differences in habitat use between kill and non-kill paths within each time interval and separated by season. Coefficient signs and significance, with non-kill paths as the reference group are reported. Coefficients are not significant unless indicated.

(“*” $P < 0.05$, “**” $P < 0.01$, “***” $P < 0.001$)

Interval (minutes)	**Proportion of forest**		**Terrain ruggedness**		**Slope**		**Distance to roads**	
	Summer	**Winter**	**Summer**	**Winter**	**Summer**	**Winter**	**Summer**	**Winter**
-90	-	-	-	-	+	+	-	+
-75	-	-	+	+	-	-	-	+
-60	-	+	-	+	+	-	-	+
-45	-	+	-	-	-	+	-	+
-30	- *	-	+	-	-	+	-	+
-15	- ***	-	+	+	-	-	-	+

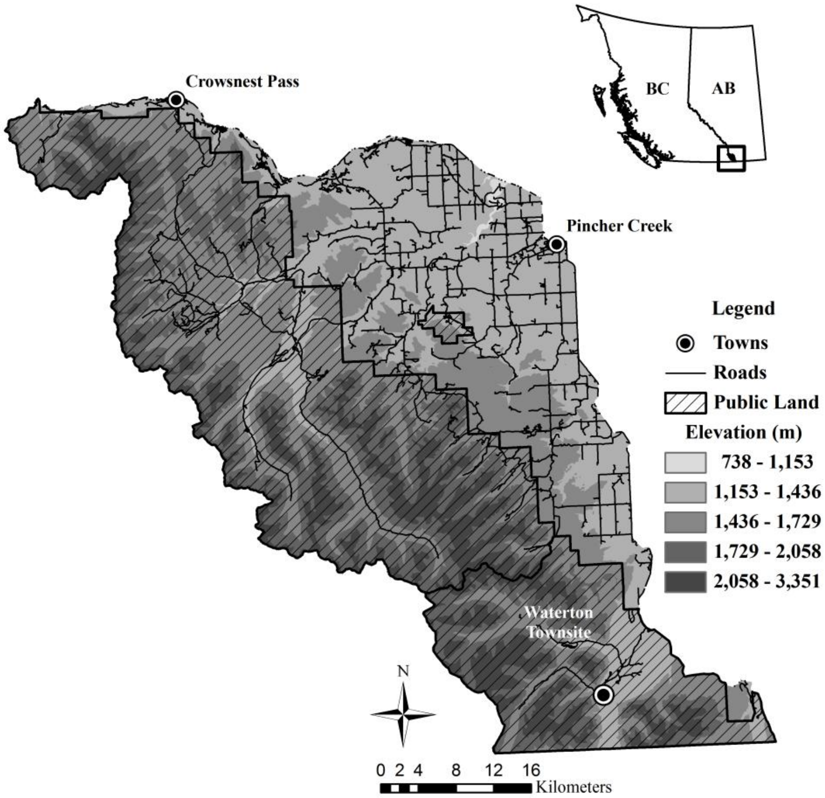

Figure 3. 1. Map of the study area in south-western Alberta, Canada. Public lands include Waterton Lakes National Park, Beauvias Provincial Park and the Castle Special Management Area.

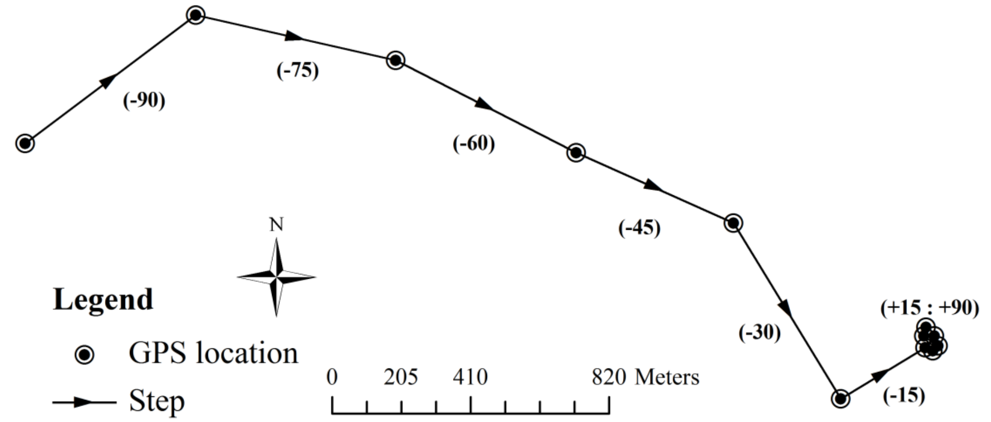

Figure 3. 2. An example of a pre-cluster path joined to 6 within cluster steps. Steps are labeled according to the time they occurred relative to the start of the cluster (time = 0).

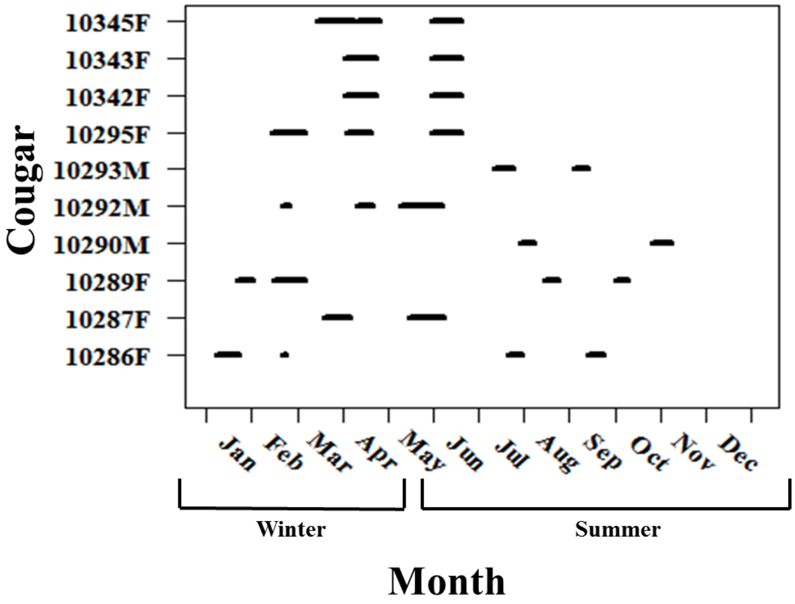

Figure 3. 3. Approximate dates of 15 minute monitoring periods per individual cougar (n = 10). Cougars are labeled by identification number and sex. Winter (Nov. 16 – Apr. 15) and summer (Apr. 16 – Nov. 15) seasons are denoted by black bars along the horizontal axis.

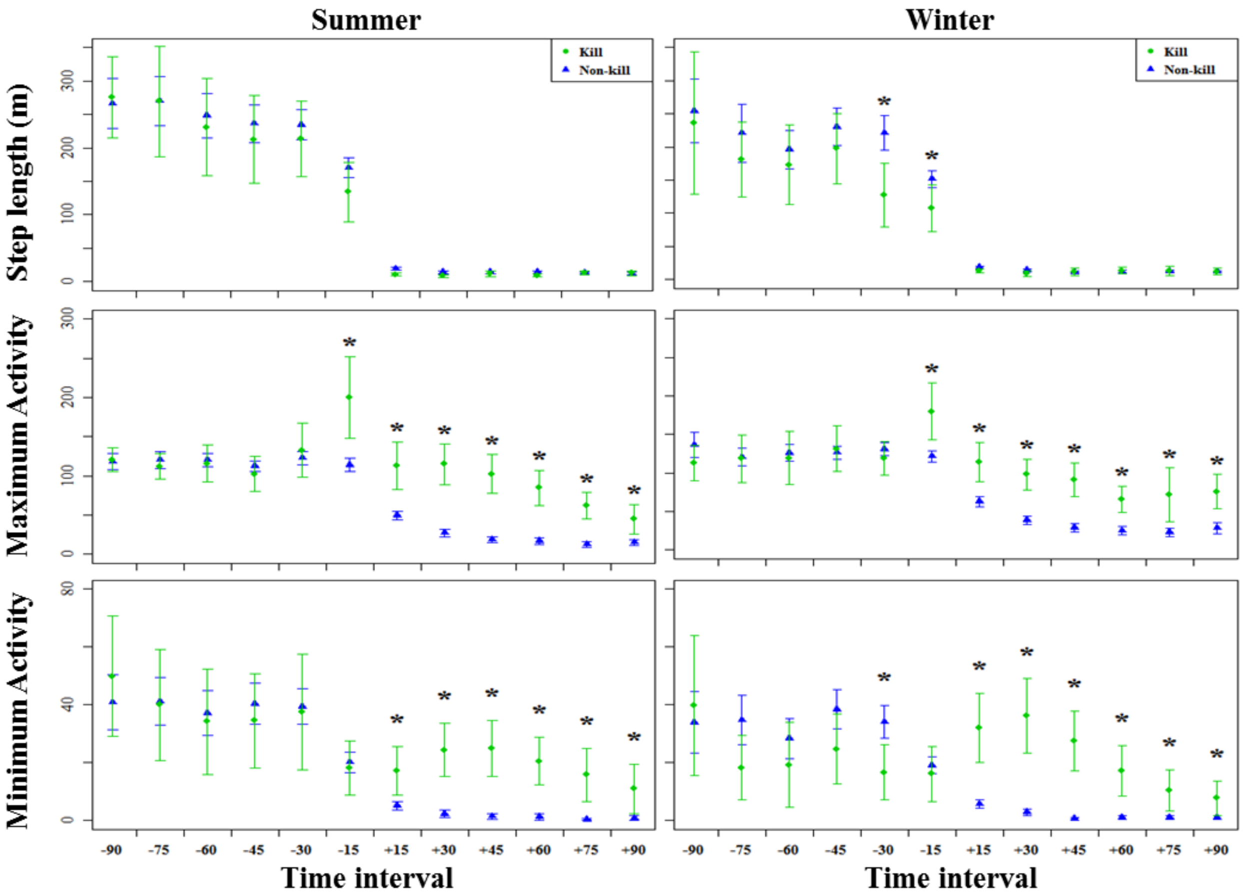

Figure 3. 4. Mean step lengths and maximum and minimum activity values for kill (circles) and non-kill (triangles) paths and clusters within each time interval and separated by season. Error bars represent 95% confidence intervals.

* Denotes significant difference ($P < 0.05$) between kill and non-kill paths within the interval.

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.

Bank, M. S., and W. L. Franklin. 1998. Puma (*Puma concolor patagonica*) feeding observations and attacks on guanacos (*Lama guanicoe*). Mammalia 64:599-605.

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

Bothma, J., and E. LeRiche. 1984. Aspects of the ecology and the behaviour of the leopard (*Panthera pardus*) in the Kalahari desert. Koedoe Supplement:259-279.

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.

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 of the United States of America 105:19114-19119.

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

Holmes, B. R., and J. W. Laundre. 2006. Use of open, edge and forest areas by pumas (*Puma concolor*) in winter: are pumas foraging optimally? Wildlife Biology 12:201-209.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. Wildlife Monographs 21:5-39.

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

Knopff, K. H. 2010. Cougar predation in a multi-prey system in west-central Alberta. University of Alberta, Edmonton, Alberta, Canada.

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.

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.

Koford, C. 1946. A California mountain lion observed stalking. Journal of Mammalogy 27:274-275.

Krumm, C. E., M. M. Conner, N. T. Hobbs, D. O. Hunter, and M. W. Miller. 2010. Mountain lions prey selectively on prion-infected mule deer. Biology Letters 6:209-211.

Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. Journal of Wildlife Management 63:901-910.

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.

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.

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

Mattson, D. 2007. Mountain lions of the Flagstaff uplands: 2003-2006 progress report. . USGS.

McKenzie, H., M. Lewis, and E. Merrill. 2009. First Passage Time Analysis of Animal Movement and Insights into the Functional Response. Bulletin of Mathematical Biology 71:107-129.

McKenzie, H., 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.

McPhee, H. M., N. F. Webb, and E. H. Merrill. 2012. Time-to-kill: measuring attack rates in a heterogeneous landscape with multiple prey types. Oikos 121:711-720.

Merrill, E., H. Sand, B. Zimmermann, H. McPhee, N. Webb, M. Hebblewhite, P. Wabakken, and J. L. Frair. 2011. Building a mechanistic understanding of predation with GPS-based movement data. Philosophical Transactions of the Royal Society B-Biological Sciences 365:2279-2288.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes, effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462-472.

R Development Core Team. 2008. R Foundation for Statistical Computing Vienna, Austria.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23-27.

Robinette, W., J. Gashwiler, and O. Morris. 1959. Food habits of the cougar in Utah and Nevada. Journal of Wildlife Management 23:261-273.

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

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

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.

Sand, H., P. Wabakken, B. Zimmermann, O. Johansson, H. C. Pedersen, and O. Liberg. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? Oecologia 156:53-64.

Turchin, P. 1998. Quantitative analysis of movement. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

Van Moorter, B., D. R. Visscher, C. L. Jerde, J. L. Frair, and E. H. Merrill. 2010. Identifying movement states from location data using cluster analysis. Journal of Wildlife Management 74:588-594.

Wilmers, C. C., E. Post, and A. Hastings. 2007. The anatomy of predator-prey dynamics in a changing climate. Journal of Animal Ecology 76:1037-1044.

Wilson, P. 1984. Puma predation on guanacos in Torres-del-paine National Park, Chile. Mammalia 48:515-522.

Young, S. P., and E. A. Goldman. 1946. The puma, mysterious American cat. The American Wildlife Institute, Washington DC.

Zimmermann, B., P. Wabakken, H. Sand, H. C. Pedersen, and O. Liberg. 2007. Wolf movement patterns: a key to estimation of kill rate? Journal of Wildlife Management 71:1177-1182.

CHAPTER 4: GENERAL CONCLUSIONS

GENERAL CONCLUSIONS

During the 1970's, cougars were reclassified from a bountied predator to a game species across North America (Sunquist and Sunquist 2002). Over the past 40 years, regulatory protection combined with changing attitudes toward large carnivores (Kellert et al. 1996) allowed cougar populations to increase and consequently expand into Midwestern North America (LaRue et al. 2012). Growing human populations are simultaneously encroaching into occupied cougar habitat in the form of roads and housing developments (Frair et al. 2008, Kertson et al. 2011). Provincial and state wildlife agencies are responsible for maintaining healthy ungulate and cougar populations, while also minimizing human-cougar encounters and risks to livestock and pets (Montana Fish Wildlife and Parks 1996, Rachael and Nadeau 2002, Wyoming Game and Fish Department 2006, South Dakota Game Fish and Parks 2010). As both human and cougar populations continue to grow and increasingly interact, ensuring the long-term persistence of cougars and their ungulate prey will become more challenging.

In this thesis I provided information for managers seeking to balance the needs of cougars with the wishes of humans, in a human-dominated landscape. My objectives were to 1) increase our knowledge of how cougars might respond to roads and traffic (Chapter 2), which will inevitably increase with the growing human population and 2) document the cougars dominant predatory strategy (Chapter 3), which could help managers predict the effects of the growing cougar population on herds of ungulate prey.

In chapter 2, I used resource selection functions to examine day and night-time cougar habitat selection alongside roads of varying traffic volumes. I was interested in whether the addition of data from roads and traffic would better explain cougar habitat selection, than information from the landscape alone. I hypothesized that cougars would use the surrounding landscape to buffer themselves from roads with greater traffic volumes. My results supported this hypothesis and cougars appeared to insulate themselves from all roads, irrespective of traffic, during the day, and roads with >1 vehicle/hour at night. Cougars buffered themselves from roads and traffic primarily by selecting areas of rugged terrain. However, if rugged terrain was unavailable cougars selected areas farther from roads with higher traffic. Interestingly, selection for rugged terrain declined in areas increasingly distant from roads, indicating that roads and traffic may force cougars to use areas more rugged than they would prefer. Never-the-less, the night-time ambivalence to roads with <1vehicle/hour combined with the day-time selection for areas close to roads, provided the terrain was sufficiently rugged, points to an underlying attraction to roads. I attributed this attraction to prey distribution, as deer, the cougar's primary prey, have been documented using roadside habitats as a refugium from predators (Muhly et al. 2011).

For managers faced with expanding road networks, consideration should be given to the landscape surrounding a road. If the landscape surrounding a road is even slightly rugged, cougars are less likely to be displaced by roads. However, the increase in selection for rugged terrain prompted by roads and traffic could affect the cougar's ability to detect prey and ultimately influence predator-prey dynamics. Indeed, the night-time lack of selection for rugged terrain alongside roads with <1 vehicle/hour substantiates the possibly of this effect, as cougars are thought to be hunting when active at night (Beier et al. 1995). Although additional research is required to determine the influence of roads on cougar-predation patterns, managers seeking to mitigate the effects of roads at night could consider access management (the control of road access) to limit traffic to <1 vehicle/hour.

In chapter 3, I used GPS telemetry relocations, radiocollar activity data, and data collected from field visits to GPS clusters to examine cougar predation behaviour. More specifically, I contrasted step lengths and activity data at unique time intervals leading to kill and non-kill clusters to test whether cougars were stalking or ambush predators. My results supported the hypothesis that cougars were primarily stalking predators, moving about the landscape to locate, stalk and kill prey. Step lengths were shorter ~30 minutes prior to a kill cluster consistent with the slow movements of a stalk. Maximum activity values showed a sudden increased in the 15 minute interval prior a kill cluster and I attribute this to the cougar attacking a prey. Minimum activity values did not indicate a pattern during the movements leading to a cluster. However, activity within clusters was greater for kill clusters, suggesting that kills generally occurred prior the start of the cluster and cougars were not waiting to ambush prey. Despite the lack of differences in the minimum activity values, I considered my results sufficient to conclude that cougars predominantly employed a stalking style of predation.

As active predators, cougars should be capable of selecting vulnerable prey, and this expectation is supported by previous studies (Kunkel et al. 1999, Pierce et al. 2000, Knopff et al. 2010). Managers assessing the impacts of cougar predation on ungulate populations should recognize that cougars are more likely to select vulnerable prey than previously thought. Finally, my results support the assumption that cougars kill prey in the interval preceding a kill cluster. For managers modeling cougar kill rate or functional response, the common procedure of using kill clusters to distinguish handling time from search time is justified.

LITERATURE CITED

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

Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. Journal of Applied Ecology 45:1504-1513.

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

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

Kertson, B. N., R. D. Spencer, J. M. Marzluff, J. Hepinstall-Cymerman, and C. E. Grue. 2011. Cougar space use and movements in the wildland-urban landscape of western Washington. Ecological Applications 21:2866-2881.

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.

Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. Journal of Wildlife Management 63:901-910.

LaRue, M. A., C. K. Nielsen, M. Dowling, K. Miller, B. Wilson, H. Shaw, and C. R. Anderson. 2012. Cougars are recolonizing the midwest: Analysis of cougar confirmations during 1990–2008. Journal of Wildlife Management in press.

Montana Fish Wildlife and Parks. 1996. Management of mountain lions in Montana. Helena, Montana, USA.

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.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes, effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462-472.

Rachael, J., and S. Nadeau. 2002. Idaho mountain lion management plan. Idaho Department of Fish and Game, Boise, Idaho, USA.

South Dakota Game Fish and Parks. 2010. South Dakota mountain lion management plan. South Dakota Division of Wildlife, Pierre, South Dakota,USA.

Sunquist, M. E., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinios, USA.

Wyoming Game and Fish Department. 2006. Wyoming mountain lion management plan. Wyoming Game and Fish Department, Lander, Wyoming, USA.