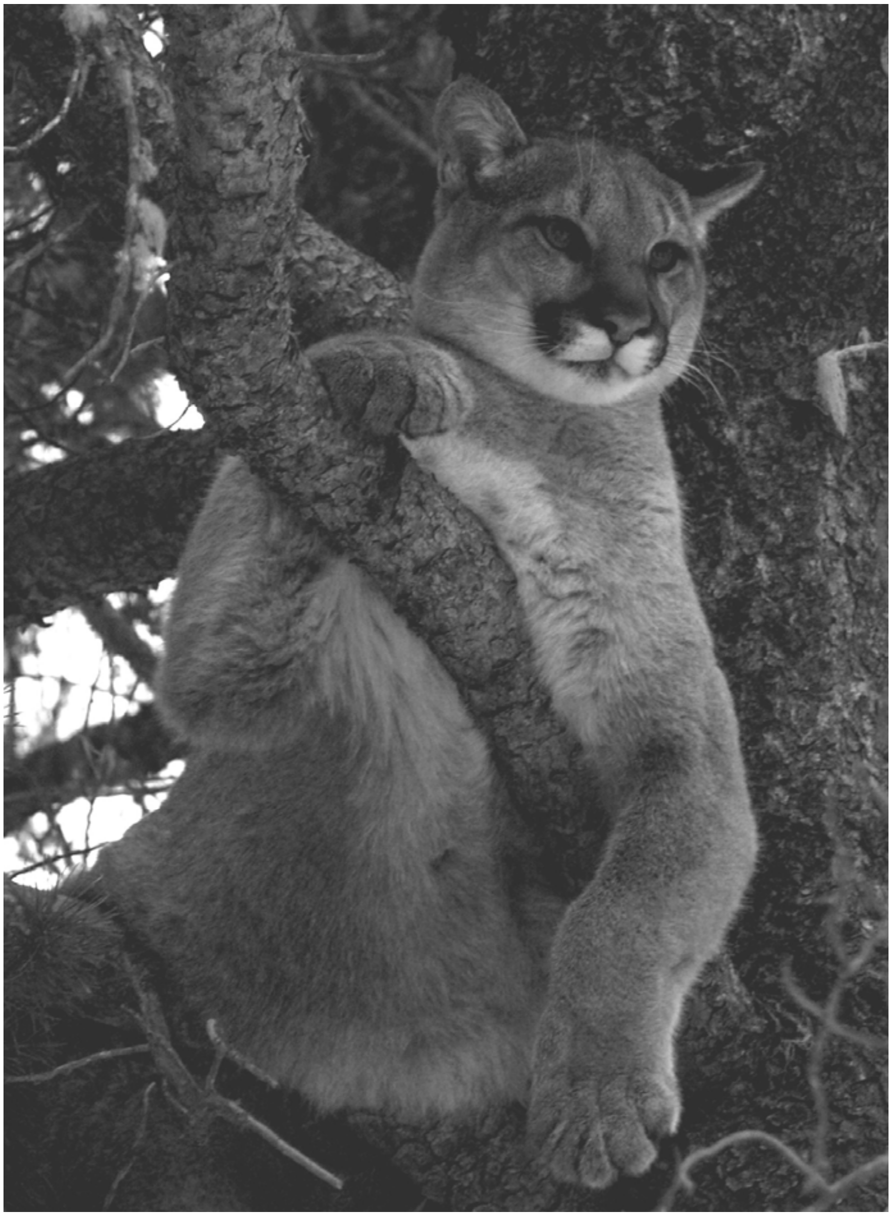

Photo: Aliah Adams Knopff

A cougar (Puma concolor) treed by hounds in west-central Alberta

University of Alberta

Cougar Predation in a Multi-Prey System in West-Central Alberta

by

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ABSTRACT

Predation by cougars (*Puma concolor*) variously can structure ecosystems and preserve biodiversity, engender conflict where livestock and pets are killed, and even drive prey populations to extinction. Effective management requires a firm grasp of the ecological drivers of predation, but these remain poorly understood due to difficulty obtaining sufficient data. My objective was to test hypotheses about drivers of predation in a population of wild cougars foraging in a multi-prey system in west-central Alberta, Canada. To obtain necessary data, I began by refining Global Positioning System (GPS) telemetry cluster techniques to monitor predation. I found that models alone were insufficient and that field visitation was required to estimate kill rate and prey composition accurately, but logistic regression models could direct field-work to improve efficiency, permitting continuous monitoring of cougar predation and generating large sample sizes. I assessed the role of scavenging as a foraging strategy and found that cougars scavenged opportunistically, reducing predation when carrion availability was high. Scavenging also made cougars susceptible to incidental snaring at wolf bait stations, and survival analysis revealed important consequences for cougar population trajectory and harvest management. I evaluated competing hypotheses about the magnitude of cougar predation and the influence of season and prey vulnerability on kill rate and prey composition. Cougars were effective predators, killing ungulates at rates near the upper end of the previously reported range. Cougar kill-rate increased by a factor of 1.5 in summer and cougars shifted prey composition seasonally as predicted by the juvenile and reproductive vulnerability hypotheses. Analysis of a multi-species functional response (MSFR) revealed that cougar impact on small populations of endangered prey is reduced by a tendency towards prey-switching but can be aggravated by the presence of individual specialists. Contrary to expectation, cougar MSFR was not driven by prey density, but rather by cougar demography and relative abundance of various prey. Finally, I reject the notion that cougars are nocturnal ambush predators, demonstrating instead that they hunt actively and make kills frequently during the day, exhibiting activity patterns loosely tied to those of their prey. I discuss the application of my findings for management and conservation.

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The data for this thesis were collected in a truly collaborative fashion. Obtaining them required the patience, determination, skill, time, sweat, and money of dozens of individuals and organizations. Without their assistance, the Central East Slopes Cougar Study would not have been possible. I have done my best to thank all of the contributors and collaborators here and I extend my sincerest apologies to anyone I might have missed. Whether listed here or not, all of those who assisted me greatly improved the quality of this work. The errors are, of course, entirely my own.

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The amount of fieldwork required to collect the data presented herein went far beyond what Aliah and I could accomplish on our own. We needed help, and lots of it! Teams of volunteers worked with us year round and put in a Herculean effort to ensure that captures went smoothly, kills were visited, cougars were monitored, and data was meticulously recorded and carefully stored. Kaitlin Byrick, Caroline Albert-Gonrand, Kelly Horton, Juniper Ross, Bram Houben, Bouke Batema, Eric Heinz, Sarah Jordan, Elyssa Collins, Stephanie Fuller, Matt Nickols, Wes Watts, Peter Knamiller, Carl Morrison, Mathieu McCann, Scott Harter, Jaclyn Comeau, Preston Taylor, Tasha Eyk, Marci Johnson, Katie Nelson, Leah Yandow, Naghma Malik, Olivia Bartlett, Örjan Johansson, Lou McNutt, Jenny Hauer, Peter Alexander, Brian Lunardi, Bram Van Moorter, Carmen Vanbianchi, Nate Libal, Deb Martel, and Marius Myrvold each spent several months volunteering with the project and collectively they invested >34,000 volunteer hours into this research. Anthony Bertrand, Dominic Grenier, Blaine Wilk,

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This project benefited greatly from the strong and unwavering support of Alberta Sustainable Resource Development. In particular, I thank SRD employees Jim Allen, Rob Corrigan, Anne Hubbs, Eldon Bruns, Dave Christiansen, John Day, Mark Hoskins, Toni Brooks, Lori Backen, and Yvette Choma for sharing data and providing advice and logistical support.

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Although I did all of the writing and analyses for each chapter and appendix included here, manuscripts have been and will be submitted for publication in collaboration with co-authors who contributed substantially to data collection, helped edit manuscripts for concision and clarity, and/or assisted with idea generation. My supervisor, Mark Boyce, is a co-author on most manuscripts. Aliah Knopff is co-author on manuscripts derived from chapters 2, 3, 4, Appendix II, and Appendix III, three of which (chapters 2, 3, and 4) appear (or are forthcoming) in the Journal of Wildlife Management. Mike Warren provided substantial assistance with computer programming and algorithm development for chapter 2, and is a co-author on that paper. Andrea Kortello is a co-author on a version of Chapter 3, for which she graciously shared the data she and her colleagues collected on cougar predation in Banff National Park during 1998-2003. Dr. Sandie Black, veterinarian at the Calgary Zoo, performed cougar necropsies and helped interpret histology results for inclusion in Appendix II, and is a coauthor on that paper. Michelle Bacon provided data for, and is co-author on, a version of Appendix III published in Wild Felid News. Nate Webb and I collaboratively developed the prey distribution and abundance layers used in Chapter 5, and Nate is a co-author on a submitted version of Appendix I. I am also very grateful to Jaqui Frair and Evie Merrill for providing me with the elk GPS data I used in Chapter 6. Thus, although I use the pronoun “I” for consistency throughout this thesis, “we” would be more appropriate in many cases.

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Finally, I would like to pay tribute to the wild places of west-central Alberta where I worked, and especially to the cougars with which I worked. The beauty, power, and incredible complexity of these animals and the landscapes they inhabit continue to astound and inspire me. At times, subjects such as these seem to defy quantitative understanding, yet it is precisely this kind of understanding that we require if we are to effectively manage species and ecosystems to preserve them for the future. It is therefore my sincere wish that all the hard work and resources (financial and otherwise) spent to produce this thesis will bear fruit, and that the analyses and interpretations included within these pages will benefit the places where I worked and the animal populations with which I worked by providing a basis for improved decision making and better management.

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CHAPTER 1

GENERAL INTRODUCTION

Understanding the dynamics of predator-prey systems is a fundamental problem in ecology. Its resolution has critical application to management and conservation of both large carnivores and their prey (Messier 1994, Hayes et al. 2000, Kinley and Apps 2001, Karanth et al. 2004, Hayward et al. 2007). Despite this importance, we still lack answers to several key questions about large carnivore predation. What kind of impact can large carnivors have on populations of their prey, and how important are these effects? What causes these effects to vary? Debate and controversy about such questions continues (Van Ballenberghe and Ballard 1994, Ballard et al. 2001, Eberhardt et al. 2003, Vucetich et al. 2005). While some advocate a formal experimental approach for testing hypotheses that might resolve such debates (Boutin 1992), the financial, logistical, and socio-political constraints associated with the manipulations and controls required for large-mammal experimentation in natural ecosystems are often prohibitive.

Where controlled expermimentation is impossible, ecologists must typically rely on observation, mensurative experiments, and modeling approaches to shed light on large carnivore-prey dynamics. Field observations provide estimates of key components of predation (Hebblewhite et al. 2005a, Sand et al. 2008), while mensurative experiments help test ideas about predation processes (Messier 1994, Peterson 1999, Vucetich et al. 2002, Hebblewhite et al. 2005b). Using this information, one can model trophic interactions, estimate the impact of large carnivores on prey populations and ecosystem structure (Mills and Shenk 1992, Eberhardt et al. 2003, Festa-Bianchet et al. 2006, Laundre and Hernandez 2006), and provide predictions to guide management and conservation (Weclaw and Hudson 2004, Lessard et al. 2005, Varley and Boyce 2006). Models, however, are only as good as the data used to parameterize them. Where data are deficient, management and conservation are impeded.

Unfortunately, relevant data have often been too sparse to adequately parameterize large carnivore predator-prey models, and many of the assumptions incorporated into such models remain untested. It is not the effort or aptitude of ecologists that has been at fault, but the inherent difficulty of collecting data from such elusive, low density, and wide-ranging animals, traits that tend to result in small sample sizes and restricted monitoring intervals. Fortunately, these difficulties are now being overcome by technology.

For instance, wolves (*Canis lupus*), are among the most prolifically studied large carnivores, yet researchers have only recently been able to provide high quality descriptions of year-round predation patterns (Sand et al. 2008). The seasonal differences in predation identified by Sand et al. (2008) have important implications for estimating annual predation rates and determining the impact wolves have on prey. This discovery was made possible by technological advances, specifically in terms of telemetry. Prior to the advent of globlal positioning system (GPS) telemetry, monitoring wolf predation in summer was all but impossible, meaning that data on predation rates during half the year were lacking. Global positioning system technology has been made widely available during the last decade, and its application in wildlife telemetry collars is revolutionizing the study of large carnivore predation by permiting year-round monitoring of large numbers of individuals simultaneously.

Relying heavily on the new GPS technology, the research presented in this thesis aims to extend our knowledge and ability to model predator-prey relations for another well-studied large carnivore: the cougar (*Puma concolor*). Although our understanding of cougar predation has increased substantially over the last 4 decades, there is much that we still do not know (Ruth and Murphy 2009). This is especially true in multi-prey systems where apparent competition (Holt 1977) has been identified as a potentially important cause of declines in some ungulate populations subject to cougar predation (Kinley and Apps 2001, Robinson et al. 2002, Rominger et al. 2004). Why do some populations of alternate prey such as bighorn sheep (*Ovis canadensis*) do poorly when healthy cougar populations are present (Rominger et al. 2004) while others do well (Hornocker 1970)? Why do cougars select deer (*Odocolieus spp.*) in some places and elk (*Cervus elaphus*) in others (Hornocker 1970, Murphy 1998)? How many ungulates do cougars kill in a year: fewer than 30 (Laundré 2008), or more than 80 (Harrison 1990)? How do cougars partition this kill rate among various prey in a multi-prey system? What role does scavenging play in cougar foraging ecology and how might this affect predation? Can cougars cause populations of abundant prey such as mule deer

(*Odocoileus hemionus*) to decline (Robinson et al. 2002), or is this unlikely (Ballard et al. 2001, Laundré et al. 2006)? What might cause variation in the answers to these questions and what is the best way to manage cougar predation where it negatively affects prey? These are the questions I address in this study.

The dissertation begins by examining Global Positioning System (GPS) telemetry techniques for monitoring cougar predation (Chapter 2), providing a methodological foundation for subsequent chapters by identifying the most efficient means to generate accurate and precise estimates of predation parameters. In Chapter 3, I investigate scavenging behavior to determine whether or not cougars are consistently attracted to carrion, which has bearing on their susceptibility to being snared at wolf bait-stations established by trappers. Also in Chapter 3, I apply survival analysis to explore the effects of snaring on cougar population dynamics in west-central Alberta. Chapter 4 provides estimates of cougar kill rate and prey composition in a multi-prey system, and attempts to resolve uncertainty in the literature regarding the number of ungulates cougars kill and the influence of season, cougar demography, and prey vulnerability on kill rate and prey composition. Chapter 5 builds on this foundation and evaluates cougar multi-species functional response, including analyses of population level prey switching and prey specialization by individual cougars. My specific objective in chapter 5 was to provide information required to better manage potentially detrimental effects of cougar-mediated apparent competition. Finally, in Chapter 6, I test the hypothesis that cougars are nocturnal ambush predators. Each chapter includes a detailed discussion of the implications of my findings for conservation and management. With the exception of this introduction and some concluding remarks (Chapter 7), chapters are organized as independent, self-contained papers. Versions of chapters 2-4 are published or have been accepted for publication in the Journal of Wildlife Management at the time of this writing.

In addition to the core thesis, I also provide 7 appendices with supplementary information that should prove useful to researchers and wildlife managers. Appendix I explores cougar population increase and range expansion in Alberta during 1991-2009. Next, in Appendix II, I provide information on 4 delayed capture-related mortalities that occurred during my study, and I assess the influence of capture and collaring on the movement and predation patterns of cougars. Appendix III gives information on GPS collar failure as a result of canine puncture. Appendicies IV and V provide supplementary information on the cougars captured and collared for research purposes during my study, including monitoring duration, causes of mortality, and home range and dispersal characteristics. Finally, in appendices VI and VII, I provide supporting information for Chapter 5, identifying previously unreported problems with ratio-dependent functional response models and showing how preference can influence predator-mediated Allee effects in multi-prey systems.

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CHAPTER 2

EVALUATING GLOBAL POSITIONING SYSTEM TELEMETRY TECHNIQUES FOR ESTIMATING COUGAR PREDATION PARAMETERS

Predation is simultaneously one of the most important, controversial, and least understood aspects of large carnivore ecology and management. Even after decades of study, many of the underlying mechanisms driving predation rates continue to be a subject of debate (Abrams and Ginsburg 2000, Skalski and Gilliam 2001, Vucetich et al. 2002, Eberhardt et al. 2003), and data often are insufficient to test fundamental hypotheses regarding the effects large carnivores have on their prey (Boutin 1992). One prerequisite for resolving controversy, testing hypotheses, and developing useful models for management is to accurately estimate parameter values for behavioral components of predation. Estimates of the rate at which prey are killed (Sand et al. 2008), the selection of prey species in multi-prey systems (Robinson et al. 2002, Knopff and Boyce 2007), the age-sex structure of prey (Mills and Shenk 1992), the physical condition of prey (Husseman et al. 2003), and the spatial distribution of predation risk (Hebblewhite et al. 2005, Kauffman et al. 2007, Creel 2008) are fundamental to understanding the effects large carnivores have on prey populations and ecosystem structure. Estimating these parameters accurately is an important challenge for ecologists and wildlife managers.

To date, snowtracking and radiotracking have been the primary techniques used to intensively monitor large carnivores for estimating behavioral parameters of predation. Snowtracking can provide a detailed record of predation events but is labor intensive and can be employed only when conditions permit. Radiotracking is not limited by snow cover but also requires intense efforts in the field (e.g., Beier et al. 1995). Even when snow is available and intensive monitoring possible, sample sizes (i.e., number of individuals or groups monitored) tend to be small and monitoring intervals short. Small sample sizes and short monitoring periods can undermine inferences about the basic mechanisms of predation (Marshal and Boutin 1999), and lead to prohibitively wide confidence intervals around parameter estimates (Hebblewhite et al. 2003). Despite the importance of estimating behavioral parameters of predation for understanding predator-prey dynamics, therefore, the onerous nature of available methods has meant that quality estimates (based on appropriate sample size and sampling intensity) are rarely obtained for large carnivores.

Global Positioning System (GPS) radiotelemetry has created new possibilities to efficiently survey large carnivore predation, permitting increased sample size and monitoring duration. Because prey takes time to consume (i.e., handling time), large carnivores wearing GPS radiocollars set to an appropriate location fix interval should produce multiple location fixes in places where prey are handled. Anderson and Lindzey (2003) pioneered a technique for identifying and visiting these clusters of GPS telemetry locations to locate prey killed by cougars (*Puma concolor*) and used it to estimate kill rate and prey composition in the Snowy Range, Wyoming. Similar field-based techniques have since been developed for wolves (*Canis lupus*) in both Scandinavia (Sand et al. 2005) and North America (Webb et al. 2008). Models parameterized using initial results from field data collected during visits to clusters also have been proposed as a means to estimate parameters of predation indirectly using GPS telemetry data alone (i.e., no additional field visitation), further improving efficiency and reducing total costs of research (Anderson and Lindzey 2003, Webb et al. 2008). Models designed to estimate kill rate have been developed (Anderson and Lindzey 2003, Franke et al. 2006, Zimmermann et al. 2007, Webb et al. 2008) and models designed to estimate prey composition at the species level in multi-prey systems have been suggested (Anderson and Lindzey 2003, Webb et al. 2008) but not attempted.

Field-based techniques are generally considered useful, but correction factors might need to be employed to adjust for bias introduced when kills are not identified by GPS location clusters (Sand et al. 2005). Detection failure has not been assessed for cougars, but can be extensive for wolves, particularly for prey smaller than deer, and can occur even when the time interval between GPS location fixes is short (Webb et al. 2008). Moreover, using models to estimate kill rate has been variously considered by researchers to be useful (Anderson and Lindzey 2003, Franke et al. 2006), somewhat useful (Webb et al. 2008), and not useful (Zimmermann et al. 2007). Consequently, additional evaluation and refinement of GPS telemetry techniques for estimating large carnivore predation parameters is required to more fully assess their utility and improve upon it where possible.

I employed a large dataset of field visits to cougar GPS telemetry clusters to evaluate, refine, and expand upon both field and model-based techniques for estimating parameters of predation. My primary objectives were threefold. First, I assessed the importance for cougars of several potential sources of bias that have been explicitly or implicitly identified in recent studies of wolf kill rate. These include the potential lack of cluster creation at kill sites (Sand et al. 2005), the effect of the number of location fixes obtained by GPS collars on parameter estimation (Sand et al. 2005, Webb et al. 2008), the size of prey that can be reliably detected using GPS location clusters (Webb et al. 2008), and the selection of an appropriate probability cutoff level for logistic regression models used to identify kills from GPS data (Zimmermann et al. 2007, Webb et al. 2008). Second, I endeavored to expand on available model-based techniques by developing and evaluating models capable of predicting not only kill locations (kill rate) but also species killed at that location (prey composition) without field visitation. Third, because sampling duration can have an important influence on the confidence placed in predation parameter estimates (Hebblewhite et al. 2003), I focused on identifying the sampling duration required to accurately estimate seasonal kill rate and prey composition for individual cougars in a multi-prey system.

STUDY AREA

I studied cougar predatory behavior in a 16,900-km^2 area located along the central eastern slopes of Alberta's Rocky Mountains (centered approx. at 52°18'N, 115°48'W). The study area was bordered by Banff and Jasper National Parks to the west and extended east to the towns of Rocky Mountain House and Caroline. Rugged mountains in the west give way to rolling foothills and eventually to flat agricultural land in the east. The region's climate was characterized by warm, dry summers and cold, snowy winters. Chinook winds provided sporadic warming during winter, often resulting in complete removal of the snow-pack from south facing slopes. The study area was mostly public land with an increasing proportion of private lands in the east. It was primarily forested (63%), but rock, ice, and bare ground (14%—primarily in the mountains), and cut-blocks of various age (8%) also were important land-cover classes. Conifer forests dominated the region and were composed primarily of lodgepole pine (*Pinus contorta)* and white spruce (*Picea glauca*). Black spruce (*Picea mariana*) and tamarack (*Larix laricina*) were common in low-lying areas, and aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) were patchily distributed throughout the region. Typical under-story species were green alder (*Alunus crispa*), willow (*Salix spp.*), and rose (*Rosa acicularis*). Human recreational activity was common, especially during summer, and Alberta's oil, gas, and forestry industries were active on the landscape. Cougars in the area were managed as a big-game animal and were hunted according to a strict quota system during winter (Ross et al. 1996).

Numerous species of ungulates were potential prey for cougars, including large numbers of elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), and feral horses (*Equus caballus*). Smaller numbers of bighorn sheep (*Ovis canadensis*), woodland caribou (*Rangifer tarandus*), and mountain goats (*Oreamnos americanus*) were patchily distributed in the western portion of the study area. Large domestic ungulates (e.g., cattle and llama) were available also, primarily on private lands in the eastern portion of the study area. Non-ungulate prey were abundant and included ruffed grouse (*Bonasa umbellus*), spruce grouse (*Falcipennis canadensis*), snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), coyote (*Canis latrans*), and red fox (*Vulpes vulpes*).

METHODS

I used data from 24 cougars (15 ad F, 5 ad M, 3 sub-ad F and 1 sub-ad M) captured during winters 2005–2006 and 2006–2007. After trained hounds tracked and treed cougars, I administered 3 mg/kg Telazol and 2 mg/kg Xylazine via remote injection (University of Alberta Animal Care Protocol no. 479505). At capture I weighed, measured, sexed, and assigned cougars to one of 3 age classes (kitten, sub-ad, or ad). I estimated age using a combination of pelage spotting progression (Shaw 1986), tooth color and wear characteristics (Ashman et al. 1983, Shaw 1986), and gum-line recession (Laundre et al. 2000). I took photographs of dentition at each capture and made post-hoc comparisons to ensure consistency among estimated ages. Exact ageing (e.g., by month) was not possible, and I considered cougars kittens if they still traveled with their mothers, sub-adults from dispersal until approximately 2.5 years, and adults if >2.5–3 years. I fitted all cougars with Lotek 4400S GPS collars (Lotek Engineering, Newmarket, ON), programmed to obtain a GPS location every 3 hours, and from which I could download data remotely on demand. I monitored cougars closely between 1 December 2005 and 18 August 2007 using a combination of ground and aerial telemetry for as long as each collar remained active. During the monitoring period, individual cougars wore active GPS collars for 25−495 consecutive days ($\bar{x}$ = 191, SD = 138), resulting in 130−2,617 locations/individual ($\bar{x}$ = 895, SD = 659). I downloaded location data remotely from active GPS collars every 2–3 weeks, usually from the ground but occasionally during aerial telemetry flights.

I used Python^{tm} programming language (Python Software Foundation, Hampton, New Hampshire, USA) to develop a rule-based algorithm capable of identifying GPS location clusters from collar data. Following Anderson and Lindzey (2003), I defined a cluster spatially as ≥2 points located within 200 m of each other. The algorithm initially searched within the 200-m limit and also used a temporal screen of 6 days when identifying associated points. Two initial points fitting these space-time restrictions formed a seed cluster and the geometric center of the cluster was calculated. The program then added additional points occurring within 200 m of the geometric center and within the temporal window of 6 days to the cluster one at a time. It adjusted the geometric center with each additional point and repeated the process until no more points could be added. I allowed clusters to persist beyond the initial 6-day temporal screen provided that the difference between the last point and the next new point at a cluster was always ≤6 days. After completing these calculations, the program output a number of descriptive variables for each identified cluster. These variables included the geometric center of the cluster, largest distance from the geometric center to a point (cluster radius), number of location fixes occurring within 200 m of the geometric center, number of fixes obtained while the cluster persists, and number of 24-hr periods where ≥1 fix was obtained at the cluster.

I programmed geometric centers into handheld GPS units and used these to locate clusters in the field. Ground crews of ≥2 people conducted systematic searches at each cluster location. Crews searched clusters with a radius of ≤50 m by walking 8 transect lines along cardinal compass bearings (e.g., N, NE, E) out to 50 m, walking 20 m to the right, and then zig-zaging back to cluster center. For clusters with a radius of >50 m I employed the same 8-line technique out to 50 m and then made concentric circles varying between 5 m and 10 m apart (depending on visibility) out to the full extent of the cluster radius (up to 200 m). I assigned a kill to a GPS location cluster if I found both prey remains that closely matched the dates over which the cluster was created and evidence of cougar feeding behavior (e.g., carcass had been buried, hair mat at cache site, multiple cougar scats). I assigned cougar scavenging to clusters where the carcass clearly had been killed by something other than a cougar (e.g., remains from a wolf-killed, hunter-killed, or road-killed animal) or if the carcass age differed greatly from the dates the cougar spent at the cluster. Using this classification scheme, instances of scavenging on fresh carcasses that were not obviously killed by something other than a cougar could be misclassified as a kill. I closely examined all found remains (scavenging or kills) to determine species, age, sex, and condition (marrow fat).

In their pioneering work, Anderson and Lindzey (2003) failed to address the potential that clusters might not form at some cougar kill locations. To evaluate the ability of GPS collars with a 3-hour fix interval to identify locations where cougar-killed prey by creating clusters, I snowtracked collared cougars prior to downloading GPS data and subsequently compared kills found during snow-tracking sessions to GPS data to determine whether clusters were consistently created at kill sites.

Model Development

I used logistic regression (Hosmer and Lemeshow 2000) to model presence or absence of a kill at a GPS cluster. I was primarily interested in producing a model capable of predicting ungulate kill rate without resorting to field visitation, but because I wanted a general model for all cougars in all seasons and did not want to miss ungulate neonates in spring, I coded all kills of prey weighing >8 kg as kills (1) and all clusters where I found either nothing or prey <8 kg as non-kills (0). Accordingly, unlike other attempts to develop logistic regression kill rate estimators for large carnivores using GPS location data (i.e., Anderson and Lindzey 2003, Zimmermann et al. 2007, Webb et al. 2008), I incorporated moderate-sized non-ungulate prey (e.g., beaver, porcupine, coyote) into model development. I did not use data from clusters truncated by initial collaring or collar removal or failure in model development. In addition, I removed clusters created at nursery sites where females had kittens. Nursery clusters can be easily screened from a dataset, even without on-the-ground visitation, because of the distinctive pattern of prolonged use (often >1 month) and creation of subsidiary clusters of shorter duration (often kills) with repeated movement between these clusters and the nursery site (Beier et al. 1995, Benson et al. 2008).

I developed a candidate set of predictive models based solely on cougar movement behavior at clusters. Although there is evidence that habitats at large carnivore kill sites differ from habitats at locations associated with other behavioral states (Kauffman et al. 2007), I wanted the model to be as broadly applicable as possible and so did not include site-specific habitat covariates in model development. I used 5 potential explanatory variables output by my clustering program: 1) duration of cluster (hr); 2) number of points at the cluster (corrected to account for variation in fix success by dividing by the proportion of successful fixes obtained while the cluster persisted); 3) fidelity to the cluster site (points at cluster minus points away over the duration of the cluster); 4) number of 24-hr periods during which I recorded ≥1 location point at the cluster; and 5) a binary variable dividing clusters into those with points spanning >1 24-hr period and those with all points occurring within 24 hr. I developed candidate models using various combinations of the predictor variables. To avoid multicollinearity I did not use highly correlated predictor variables (i.e., $|r| > 0.7$) in the same model. Because the small sample size correction for Akaike's Information Criterion (AICc) converges to AIC at large sample sizes, it can be applied for model selection regardless of sample size, and I used it to identify a top model from my candidate set (Burnham and Anderson 2002).

The probability output from the logistic regression model at which a cluster is assigned kill or non-kill status can be set arbitrarily, most commonly at 0.5 (e.g., Zimmermann et al. 2007), or it can be defined by using sensitivity and specificity curves to obtain an optimal output (e.g., Webb et al. 2008). Cutoff selection can determine whether the model performs well or poorly at prediction (Hosmer and Lemeshow 2000) and might affect kill rate estimation. I investigated the effect of using 4 different cutoff levels (0.5, 0.4, 0.3, and the optimum derived from the data) on kill-rate estimation. I evaluated model classification using receiver-operator characteristic (ROC) curves. Next, I assessed the ability of the model to predict kill rate at the various cutoff levels using *k*-fold cross validation with 5 data partitions (Boyce et al. 2002). Other studies test the generality of kill rate models within a study area by withholding data (usually from an individual or a small subset of individuals), testing the ability of the model to predict kill rate for the withheld data, and then either re-fitting the model by incorporating withheld data (Anderson and Lindzey 2003) or leaving testing data out of final model parameterization entirely (Webb et al. 2008). *K*-fold may be a more appropriate technique because prediction is evaluated based on a representative sample of the population instead of a potentially unrepresentative single animal or small subset of animals. Moreover, the *k*-fold technique permits use of all available data for initial model selection (i.e., data are withheld only when assessing prediction, not when identifying a top model).

I also explored the possibility that prey composition might be estimated using model based (i.e., indirect) methods. I assigned all prey >8 kg located at clusters to one of 5 prey types: deer (white-tailed and mule deer combined), elk, moose, feral horses, and other (all other prey). I developed multinomial logistic regression models (Hosmer and Lemeshow 2000) to assign a probability that a given kill cluster fell into one of these categories. For model development I used only data from clusters where I found a kill and could unambiguously assign it to one of these prey categories. I developed a candidate set of models based primarily on cluster variables associated with duration and intensity of use (no. of points, fidelity, and binary day periods), reasoning that larger prey would result in longer handling times for cougars (Anderson and Lindzey 2003). I also used information about individual cougar because cougar age (sub-ad vs. ad) and especially sex (M vs. F) have been suggested to contribute to prey selection (Ross and Jalkotzy 1996, Murphy 1998, Anderson and Lindzey 2003). Finally, I risked reducing broader model applicability by incorporating site-specific habitat covariates extracted from a Geographical Information System (GIS) because I assumed that different habitat selection patterns exhibited by different ungulate prey types might be a critical component of effective discrimination of species killed. I used deer as the reference category in model development and I selected a top model using AICc. The multinomial model output a set of probabilities, one for each possible category of kill (Hosmer and Lemeshow 2000). The category with the highest probability was the predicted category. Just as with the logistic models, I used 5-fold cross validation to assess the predictive capacity of the top multinomial prey composition model.

Assessing the Influence of Fix Success and Improving Efficiency in the Field

Low and variable GPS location acquisition rates are common problems encountered in GPS radiocollar studies of cougars (Anderson and Lindzey 2003, Land et al. 2008). Lower than average GPS acquisition might reduce the probability of cluster creation at some kills, biasing estimates of kill rate and prey composition. Webb et al. (2008) examined the effect of reducing the time between GPS location attempts (fix interval) on the probability of locating wolf-killed prey and found that kill rate for small prey was underestimated at longer fix intervals. Variation in fix acquisition, however, presents a different problem. Reductions in fix success are more likely to approximate a random loss of data, as opposed to the strictly systematic data reduction as the fix interval is lengthened. This type of fix loss can contain runs of missed points, a pattern that may be even more likely to result in detection failure. To assess the extent to which reduced fix success biases cougar kill rate and prey composition, I used data from 4 collars that obtained above average fix success (>60%; see results) and were deployed on cougars for ≥11 months. I randomly removed fixes to simulate reduced GPS acquisition at 3 levels (45%, 30%, and 15%). I then re-ran the clustering algorithm at each reduced level to determine how many clusters were lost and the number of kill clusters lost. I also used the logistic regression model at the optimal cutoff level to identify changes in the number of kills predicted by the model as fix success declined. Finally, I examined changes in prey composition at each level of GPS acquisition reduction.

In cases where detailed information is required about large carnivore predation events, there may be no substitute for field visitation. Hence, I assessed the potential for statistical models to help guide cluster visitation and improve the efficiency of field-based parameter estimation for cougars. I used the top logistic regression model to output the probability that each cluster I visited represented a kill. I then simulated various cutoff probabilities below which I would not have visited a cluster in the field. I assessed amount of effort saved and proportion and type of kills missed at each simulated probability cutoff. Because availability of smaller prey (e.g., ungulate neonates, beaver) was reduced in winter and I expected that handling times might be longer in winter due to slower meat spoilage, I also examined the effect of season on cutoff selection for cluster visits.

Next, I explored the effect of sampling duration on estimates of kill rate and prey composition. My goal was to identify the minimum duration of intensive monitoring required to provide estimates of cougar kill rate and prey composition close to the true values obtained from long-term monitoring. Because inferences about kill rate and prey composition often pertain to either summer or winter in seasonal environments, I investigated the sampling intensity required to provide estimates for 1 season (180-day period). I used resampling procedures to simulate various sampling intensities from the first 180 days for each of 10 cougars that I continuously monitored for ≥180 days. I randomly generated 10 samples for each cougar at each of 10 sampling intensities, increasing at intervals of 10% up to 180 days (e.g., 18 days, 36 days, 54 days, … ,180 days). Thus, I generated 1,000 simulated monitoring periods. I obtained percent error in kill rate (KR_{kj}) for simulations at the k^{th} sampling intensity for the j^{th} cougar using:

$$KR_{kj} = \frac{\left(\sum_{i=1}^{n} | \hat{x}_i - X_j |\right)/n}{X_j} \qquad \text{(Equation 2.1)}$$

where $\hat{x}_i$ = kill rate of the i^{th} simulated monitoring period at the k^{th} sampling intensity for the j^{th} cougar, X_j = kill rate for the j^{th} cougar obtained over the full 180-day intensive monitoring period, and n = number of simulated monitoring intervals generated at the k^{th} sampling intensity. I calculated mean error in prey composition (PC_{kj}) using:

$$PC_{kj} = \frac{\sum_{i=1}^{n} \left(\frac{\sum_{l=1}^{m} | \hat{y}_l - Y_{lj} |}{2} \right)}{n} \qquad \text{(Equation 2.2)}$$

where $\hat{y}_l$ = estimated percentage of the l^{th} prey type in the i^{th} simulated monitoring period at the k^{th} sampling intensity for the j^{th} cougar, Y_{lj} = percentage of the l^{th} prey item in the diet of the j^{th} cougar obtained over the full 180-day intensive monitoring period, m = number of prey items in the j^{th} cougar's diet, and n = number of simulated monitoring intervals generated at the k^{th} sampling intensity. I then calculated the mean error and confidence limits for kill rate and prey composition at each sampling intensity using KR_{kj} and PC_{kj} of all 10 cougars. I tested the hypothesis that the relationship between sampling intensity and mean error would be nonlinear (i.e., error would decline rapidly over initial increases in sampling intensity and then deliver diminishing returns at higher sampling intensities) by using one-tailed t-tests to compare residuals of the best fit linear and quadratic curves.

RESULTS

I visited 1,735 GPS location clusters identified using the rule-based clustering algorithm for 24 instrumented cougars (mean clusters/cat = 72.3, SD = 53.5). On average, field crews visited clusters 21 days after they were made (SD = 14.9) and the maximum time between cluster creation and cluster visitation was 144 days. In total, crews spent 1,508 hours searching at cluster locations. If kills were present they were usually found quickly, in many cases before a systematic search was implemented. On average, 0.6 hours of searching were required to locate a kill and 1.0 hours to conclude absence of a kill at a cluster. I found cache sites (location where a cougar buried and consumed prey), on average, within 27.1 m (SD = 24.7) of the geometric center of the cluster. Most time invested in obtaining data was spent getting to the cluster location.

I found 637 prey >8 kg, 30 prey <8 kg, and 37 instances of scavenging at cluster sites. Clusters where prey >8 kg were present averaged 12 locations (SD = 9.6) and spanned 71.5 hours (SD = 60.6). Even when I considered only clusters associated with non-ungulate prey <40 kg but >8 kg (*n* = 90), clusters maintained an average of 8 locations (SD = 6.0) and 52.8 hours (SD = 88.6). Once a cougar killed an animal >8 kg, it displayed high fidelity to the location where it cached the prey, with an average of 87.9% (SD = 19.7%) of GPS fixes obtained over the cluster duration occurring within 200 m of the cache site. Five species of wild ungulate (elk, moose, feral horse, mule deer, and white-tailed deer) comprised most (85.9%) prey I found at cluster locations. Beaver (4.5%) and coyote (1.5%) were the most common non-ungulate prey represented at clusters. At 14 (2.2%) clusters where predation occurred, I found >1 prey item. Most often this consisted of female ungulates and their young offspring. However, on several occasions, an ungulate and a mesocarnivore (coyote or fox that likely was scavenging from the ungulate carcass) were both killed at a cluster. I rarely (*n* = 2) recorded kills of >1 large ungulate (e.g., >1 ad). The largest number of cougar kills located at one cluster was 4 (1 ad F deer, 2 deer fawns, and 1 coyote). I probably underestimated the number of multiple kills occurring at cougar GPS clusters, however, because field crews usually stopped searching at clusters once a kill was found.

To assess the efficacy of using collars with a 3-hour fix rate to locate prey killed by cougars, I conducted 29 snowtracking sessions of collared cougars spanning >351 cougar hours of activity. During my tracking sessions I found 5 prey items killed by cougars. Four of the kills were deer (2 of which were fawns aged 5 months and 9 months), each of which had a cluster of ≥11 location fixes associated with it. The fifth kill I found was a snowshoe hare that did not have an associated cluster.

Model Performance

The top model predicting presence or absence of a kill of prey >8 kg at a cluster included covariates for the number of points at a cluster (corrected for fix success), number of day periods, fidelity to the cluster, and average distance of points from geometric center (Table 2.1). Kills were more likely to be present at clusters that had higher numbers of corrected points, at clusters where the cougar was present >1 day, at clusters for which the cougar showed high fidelity, and at clusters where the average distance from the geometric center of the cluster was smaller (Table 2.2). The optimal probability cutoff above which a cluster was considered a kill >8 kg was 0.22. The top model fit the data well with a ROC area under the curve of 0.93 (i.e., outstanding discrimination between kills and non-kills; Hosmer and Lemeshow 2000).

Table 2.1: The 5 top-ranked logistic regression models for discriminating kills (>8 kg) from non-kills at 1,735 cougar Global Positioning System location clusters along the central east slopes of Alberta's Rocky Mountains, Dec 2005–Aug 2007. Model log-likelihood (LL), number of estimated parameters (K), small sample size corrected Akaike's Information Criterion (AICc), AICc difference (Δ_{AICc}), and AIC weight (wi) are displayed.

Rank	**Variables**	**LL**	***K***	**AICc**	**Δ AICc**	w_i
1	COR_AT[a], FIDELITY [b], BIDAY1[c], AVERAGE_DI[d]	−582.180	4	1,173.3	0.00	0.82
2	COR_AT, FIDELITY, BIDAY1	−584.953	3	1,176.5	3.24	0.16
3	COR_AT, FIDELITY, AVERAGE_DI	−587.608	3	1,181.7	8.49	0.12
4	COR_AT, FIDELITY	−589.831	2	1,183.9	10.67	0.04
5	COR_AT	−635.227	1	1,272.5	99.28	0.00

[a] No. of location fixes divided by the proportion of successful fixes over the duration of the cluster.

[b] No. of fixes away from the cluster subtracted from the no. of fixes at the cluster over the duration of the cluster.

[c] Binary variable indicating 1 or >1-day period spent at the cluster.

[d] Average distance of all points at the cluster from the geometric center of the cluster

Table 2.2: Coefficients for the highest rank logistic regression model used to predict presence or absence of a kill at a Global Positioning System location cluster for cougar along the central east slopes of Alberta's Rocky Mountains, Dec 2005–Aug 2007.

Variable	Coeff.	SE	95% CI
COR_AT[a]	0.188	0.202	0.149, 0.229
FIDELITY[b]	0.112	0.014	0.085, 0.140
BIDAY1[c]	1.071	0.219	0.643, 1.500
AVERAGE_DI[d]	–0.007	0.003	–0.012, –0.001
Constant	–2.722	0.152	–3.020, –2.424

[a] No. of location fixes divided by the proportion of successful fixes over the duration of the cluster.
[b] No. fixes away from the cluster subtracted from the no. of fixes at the cluster over the duration of the cluster.
[c] Binary variable indicating 1 or >1-day period spent at the cluster.
[d] Average distance of all points at the cluster from the geometric center of the cluster.

Assessing model predictive capacity using *k*-fold cross validation at the 0.22 cutoff demonstrated that the model had high classification success (86%) and provided estimates of cougar kill rates averaging within 8.7% of the true value (Table 2.3). Conducting the *k*-fold procedure for the same model at 3 arbitrarily selected cutoff levels (0.3, 0.4, 0.5), demonstrated that choice of cutoff level had a large effect on kill-rate estimation (Table 2.3). Both the optimal cutoff (0.22) and the 0.3 cutoff provided reasonable estimates of kill rate (on average within 10% of the true value), whereas the 0.4 and 0.5 cutoffs underestimate kill rate by >16% (Table 2.3). Because clusters were more often non-kill than kill-sites, errors of false positive (incorrectly identifying a non-kill cluster as a kill) and false negative (incorrectly identifying a kill cluster as a non-kill) canceled each other out to produce better estimates of kill rate at lower cutoff levels, despite slight increases in overall classification success at higher cutoff levels (Table 2.3).

Of the 637 kills >8 kg that I found at GPS location clusters, 468 (73.3%) were deer, 47 (7.4%) moose, 38 (6.0%) elk, 21 (3.3%) feral horses, and 63 (9.9%) other prey (primarily non-ungulate). Several candidate models in the multinomial set were statistically indistinguishable in their ability to discriminate between these categories (Table 2.4). These models represent slight variations on a theme and I selected the global model containing the most variables (the second ranked model) for prediction because this model explained the most total variation (i.e., had the lowest log likelihood). The selected model included behavioral variables (no. of points at a cluster, no. of day periods spent at the cluster, and average distance of points from geometric center), individual cougar characteristics (cougar age and sex), and environmental covariates (season, wet openings, dry openings, mixed forest, clearcuts, and terrain ruggedness within a radius of 500 m from the cache site) to predict the type of kill (Table 2.5). The 5-fold cross validation I used to assess the predictive capacity of the model revealed a mean percent correctly classified of 74.8%. The model over-predicted deer (Table 2.6), which were the most abundant prey. Other prey were under-represented by the model and also were burdened with more variation in the predicted level of dietary importance (Table 2.6).

Table 2.3: Mean and standard deviation of 5-fold cross validation for percent correctly classified, rates of misclassification, and deviation from known cougar kill rate for predictions at 4 probability cutoff levels derived from logistic regression models distinguishing kill locations from non-kill locations for cougar along the central east slopes of Alberta's Rocky Mountains, Dec 2005–Aug 2007.

Cutoff	**Correctly classified**		**Rate of false positive**[a]		**Rate of false negative**[b]		**Deviation from known kill rate**	
	Mean %	SD	Mean %	SD	Mean %	SD	Mean %	SD
0.22	86.08	3.1	21.51	4.63	8.76	2.41	+8.67	5.56
0.3	87.58	1.76	14.79	1.91	11.06	2.35	−6.58	7.57
0.4	87.89	1.15	11.17	2.00	12.44	2.14	−16.11	10.21
0.5	87.60	1.6	9.37	2.90	13.58	2.12	−22.69	10.51

[a] Rate of false positive is no. of clusters incorrectly considered kills by the model divided by the true number of kill clusters.

[b] Rate of false negative is the number of clusters incorrectly considered non-kills by the model divided by the true number of non-kills.

Table 2.4: The 5 top-ranked models for discriminating prey type (deer, elk, moose, feral horse, other) at 637 cougar kills along the central east slopes of Alberta's Rocky Mountains, Dec 2005–Aug 2007. Model log-likelihood (LL), number of estimated parameters (K), small sample size corrected Akaike's Information Criterion (AICc), AICc difference (Δ_{AICc}), and AIC weight (w_i) are displayed.

Rank	Variables	LL	*K*	AICc	Δ_{AICc}	w_i
1	C_SEX[a], C_AGE[b], SEASON[c], COR_AT[d], BIDAY1[e], DNWETOP[f], DNDECMI[g], TER_RUG[h], DNNATOP[i], DNALLCU[j],	−441.097	10	907.823	0.000	0.261
2	C_SEX, C_AGE, SEASON, COR_AT, BIDAY1, AVERAGE_DI[k], DNWETOP, DNDECMI, TER_RUG, DNNATOP, DNALLCU,	−439.515	11	907.953	0.129	0.244
3	C_SEX, C_AGE, SEASON, COR_AT, BIDAY1, DNWETOP, DNDECMI, TER_RUG, DNNATOP	−442.820	9	908.135	0.312	0.223
4	C_SEX, C_AGE, SEASON, COR_AT, DNWETOP, DNDECMI, TER_RUG, DNNATOP	−444.534	8	908.581	0.758	0.178
5	C_SEX, C_AGE, SEASON, COR_AT, BIDAY1, AVERAGE_DI, DNWETOP, DNDECMI, DNCONIF[l], TER_RUG, DISTWAT	−441.277	11	911.476	3.653	0.042

[a] Cougar sex.

[b] Cougar age.

[c] Season.

[d] Number of location fixes divided by the proportion of successful fixes over the duration of the cluster.

[e] Binary day period.

[f] Wet openings.

[g] Mixed forest (deciduous and conifer).

[h] Terrain ruggedness.

[i] Natural openings.

[j] Clearcuts.

[k] Average distance of all points at the cluster from the geometric center of the cluster.

[l] Conifer forest.

Table 2.5: Coefficients for the highest ranked multinomial regression model used to predict the species of kill at a cougar kill cluster along the central east slopes of Alberta's Rocky Mountains, Dec 2005–Aug 2007. All Coefficients are in relation to deer, which is the reference category.

Variable	**Coeff.**			
	moose	**elk**	**horse**	**other**
C_SEX[a]	3.019	1.999	4.516	1.884
C_AGE[b]	1.053	1.936	16.220	-0.191
COR_AT[c]	0.026	0.013	0.003	−0.054
BIDAY1[d]	−0.466	−0.033	0.341	−0.684
AVERAGE_DI[e]	0.008	0.007	−0.004	0.008
SEASON[f]	-2.98	−0.925	−1.309	−0.351
TER_RUG[g]	−0.030	−0.010	−0.021	−0.028
DNWETOP[h]	−0.030	−0.023	−0.041	0.003
DNDECMI[i]	−0.002	0.002	0.003	−0.001
DNNATOP[j]	0.001	0.007	−0.027	0.005
DNALLCU[k]	−0.000	0.001	−0.003	−0.001
CONSTANT	-6.670	−7.528	-40.193	-2.497

[a] Cougar sex (1 = F, 2 = M).
[b] Cougar age (1 = sub-ad, 2 = ad).
[c] Number of location fixes divided by the proportion of successful fixes over the duration of the cluster.
[d] Binary day period (0 = <1-day period, 1 = >1-day period spent at the cluster).
[e] Average distance of all points at the cluster from the geometric center of the cluster.
[f] Season (0 = summer, 1 = winter).
[g] Terrain ruggedness.
[h] Wet openings.
[i] Mixed forest (deciduous and conifer).
[j] Natural openings.
[k] Clearcuts.

Table 2.6: Proportion of the true composition of each prey species predicted by the top multinomial model distinguishing prey species at cougar kill locations along the central east slopes of Alberta's Rocky Mountains, Dec 2005–Aug 2007, for each of 5 randomly assigned partitions of the data. A value of 1.00 represents correct prediction.

Species	**Partition 1**	**Partition 2**	**Partition 3**	**Partition 4**	**Partition 5**	$\bar{x}$	**SD**
Deer	1.12	1.20	1.24	1.20	1.20	1.19	0.04
Elk	0.44	0.00	0.00	0.00	0.37	0.16	0.22
Moose	1.50	0.71	0.58	0.85	0.92	0.91	0.35
Horse	1.00	0.33	0.50	0.00	0.25	0.41	0.37
Other	0.08	0.30	0.33	0.36	0.40	0.29	0.12

Assessing the Influence of Fix Success and Improving Efficiency in the Field

The Lotek GPS collars used in this chapter averaged 60% fix success, ranging from 45% to 83% for individual cougars. Simulated fix success reduction by random removal of GPS locations revealed that the number of clusters created dropped rapidly as I reduced fix success (Figure 2.1). However, clusters where kills were present were more resistant to fix success reductions than were non-kill clusters (Figure 2.1). Indeed, reducing fix success to 45% resulted in only a slight underestimate of kill rate ($\bar{x}$ =3.8%). Reductions to 30% resulted in more substantial underestimates ($\bar{x}$ =11.4%), and by the time I reduced fix success to 15% a substantial proportion of cougar kill clusters ($\bar{x}$ = 34.1%) and most non-kill clusters ($\bar{x}$ = 85.9%) were lost. The top logistic regression model using the optimal cutoff of 0.22 further underestimated the number of kill clusters by approximately 15%, regardless of the level to which I reduced fix success (Figure 2.1). Clusters associated with smaller prey such as beaver and deer were lost first as fix success declined, whereas no large ungulates such as elk, moose, or feral horses were lost from the kill sample until I reduced fix success to 15%.

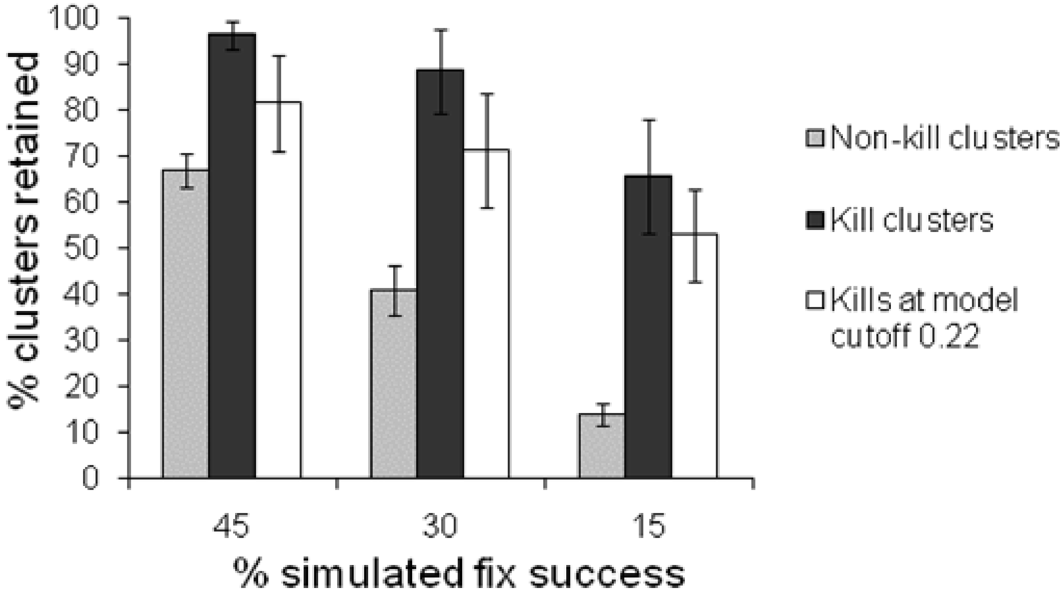

Figure 2.1: Percentage of non-kill clusters, kill clusters, and model-predicted kill clusters retained at 3 levels of simulated fix success for 680 non-kill clusters and 260 kill clusters generated by 4 cougar with >60% initial fix success in west-central Alberta, Dec 2005–Aug 2007.

Applying the top logistic regression model to my entire cluster dataset (*n* = 1,735) revealed that visiting only those kills with a probability above the optimal cutoff of 0.22 would have reduced my efforts in the field by 60% but also would have eliminated 14% (*n* = 88) of cougar killed prey from my sample. Over 80% of the eliminated prey were either ungulate young of the year (most of them in summer) or smaller non-ungulate prey such as beaver and coyote, resulting in a strong sampling bias against smaller prey if the optimal cutoff is employed. By using the more conservative probability cutoff of 0.1 to direct field visitation, on the other hand, field efforts were reduced by 23% while maintaining almost perfect documentation of kills >8 kg (98%). When I examined the kill probability output by the model at a kill cluster by season, I found that more clusters with low model probabilities were associated with kills >8 kg in summer ($\bar{x}$ = 0.686, 15 Apr–14 Oct) than in winter ($\bar{x}$ = 0.801, 15 Oct–14 Apr; 2-tailed t-test, $P < 0.001$). Consequently, in summer more clusters must be visited (model probability cutoff = 0.1) to locate ≥95% of cougar prey >8 kg than must be visited to locate the same percentage of prey >8 kg in winter (model probability cutoff = 0.15).

I found no obvious optimal level of effort that should be employed to estimate kill rate and prey composition for a season (180-day period). The relationship between mean error in kill rate and sampling intensity was linear (i.e., the best-fit quadratic equation did not differ from the best fit straight line; t-test, $P = 0.13$), indicating that each investment in time yields an approximately equal return in improved accuracy. The relationship between mean error in prey composition and sampling intensity, on the other hand, was quadratic (t-test, $P = 0.02$), but the curve was shallow and returns on time invested in the field did not diminish rapidly (Figure 2.2). Despite the lack of a clearly defined optimal level of effort that allowed accurate estimation of both parameters, it is clear that short monitoring periods produce estimates of kill rate and prey composition that are both biased and imprecise. Indeed, 108 consecutive days of monitoring were required before the upper bound of a 95% confidence interval surrounding the mean error of both kill rate and prey composition dropped below 20% (Figure 2.2).

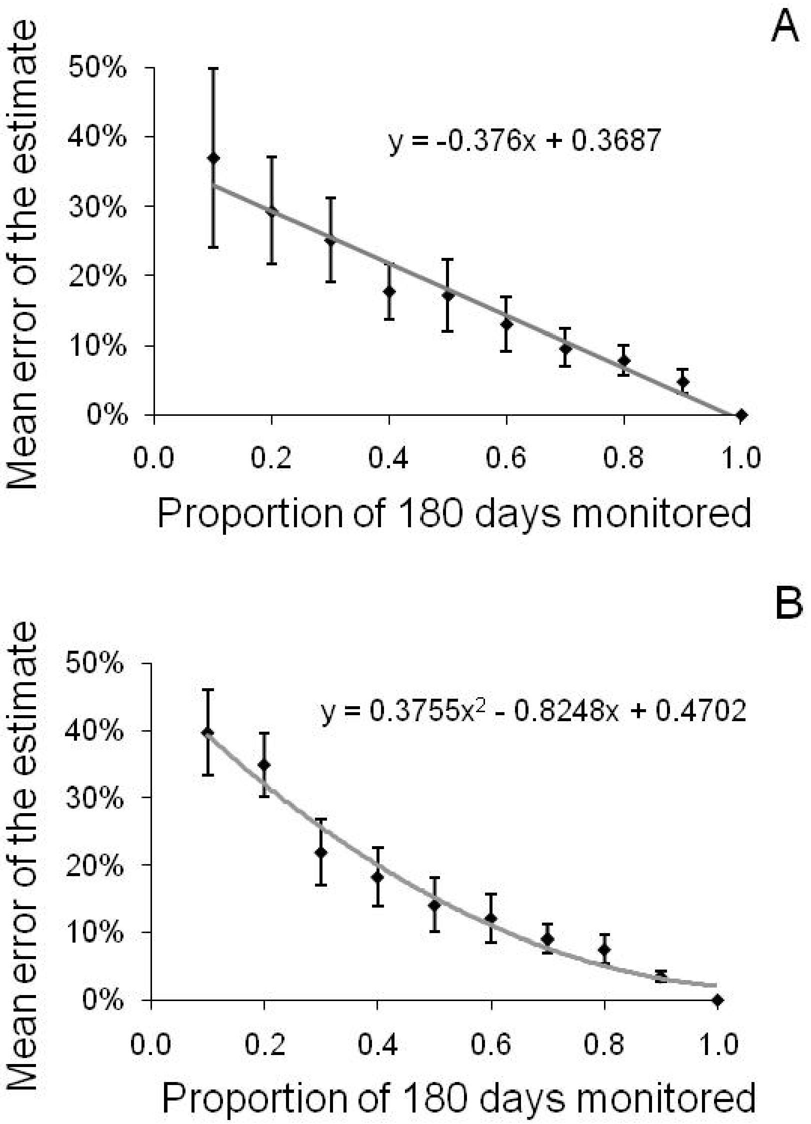

Figure 2.2: Relationship between the proportion of a 180-day period monitored and A) mean absolute error (%) in kill rate estimates and B) mean absolute error (%) in prey composition estimates obtained using 1,000 simulated sample periods drawn from continuous 180-day monitoring sessions for 10 cougar in west-central Alberta, Dec 2005–Aug 2007. Ninety five percent confidence intervals bracket each error estimate. The best fit (linear or quadratic) curve and their equations are displayed.

DISCUSSION

My rule-based clustering algorithm proved effective for identifying locations where cougars killed prey >8 kg. Webb et al. (2008) promote the use of statistical clustering programs (e.g., Kuldorff et al. 2005) for kill-site identification. However, to use these programs effectively, biologically reasonable constraints (rules) must be applied to the spatial and temporal extent of clusters they identify. In practice, therefore, statistical programs only improve on a rule-based algorithm if the statistical probability associated with the cluster output will be used in subsequent models for kill site identification. If subsequent modeling will be based on parameters not derived from the statistical program (e.g., Webb et al. 2008), then rule-based algorithms such as the one I have developed for identifying clusters serve equally well and have the advantage of outputting user-defined descriptive variables associated with the cluster (e.g., geometric center of cluster, no. of 24-hr periods at a cluster) in one step.

Although the total number of kills I located during snowtracking sessions of GPS-radiocollared cougars was small, it was encouraging to find that detection rates were high (100% of the ungulate prey had GPS location clusters associated with them). Moreover, simulated reductions in fix success demonstrated that clusters at locations where prey >8 kg were found were exceptionally robust to fix loss (due to the large number of fixes originally obtained), indicating that a cluster is likely to form at locations where prey >8 kg were handled. However, my small sample of snowtracking data for GPS collared cougars in winter and my lack of an independent evaluation technique for detection rates in summer means that further tests of this conclusion are warranted. In general, success of GPS clusters for locating cougar killed prey, even when fix success is low, is likely due to this predator's long handling times (even for prey 8–40 kg) and high fidelity to kill locations. Differences in handling behavior between solitary predators like cougars and group-hunting predators such as wolves may partially explain why recent applications of GPS telemetry for estimating wolf kill rate report much lower detection rates than I found (Sand et al. 2005, Zimmermann et al. 2007, Webb et al. 2008). I suspect that future applications of GPS cluster techniques will work best for large carnivores that, like cougars, display high fidelity to kill locations and have long handling times.

The generally low and variable fix success observed in my study is consistent with other deployments of various types of GPS collars on cougars (Anderson and Lindzey 2003, Land et al. 2008). Surprisingly, fix success did not bias kill rate or prey composition estimates until it was reduced below 45% and the bias did not become severe until it fell below 30%. While fix success on cougar GPS collars may generally be high enough for bias to be avoided when prey are handled, one might still fail to detect cougar predation events (prey >8 kg) if prey were killed but not consumed. In Scandinavia, GPS-collared wolves occasionally failed to produce location clusters at kills when human disturbance truncated prey handling (Zimmermann et al. 2007). Similar situations are possible for cougars, especially in multi-predator systems where encounter competition occurs between cougars and other large carnivores (Murphy et al. 1998, Ruth 2003). I documented several instances of wolf and bear visits to cougar kill sites, including a number of usurpations of cougar kills by dominant predators; however, most cougar displacements occurred after cougars had begun handling prey, and in only 6 cases (<1% of kills I visited) was the carcass usurped after collars obtained only 2–4 location fixes. Therefore, it is probably rare for cougars to handle prey >8 kg for such a short duration that a cluster is not generated.

Estimates of behavioral parameters of predation also can be biased if cougars consume carcasses of animals they did not kill, creating GPS telemetry location clusters at scavenging sites that are misclassified as kills. Anderson and Lindzey (2003) were unable to address the influence of scavenging on cougar kill rate estimation because of technological limitations but suggested the influence would be minor because cougars were believed to scavenge infrequently. However, this potential bias can be addressed directly by employing collars from which GPS data can be downloaded regularly to ensure the interval between cluster creation and field visitation is sufficiently short that cause of death can be identified. Using downloadable collars, I was able to identify 37 clear instances of scavenging (approx. 5% of all clusters where I found carcasses) and remove these from my kill sample, diminishing the effect of this form of bias.

Finally, the simple act of measuring or marking has been shown to affect the quality of inference that can be made in certain ecological studies (Cahill et al. 2001, Jackson and Wilson 2002). The GPS collars I used were not especially heavy (<2% of cougar bodyweight) but were bulky. If wearing a collar did affect cougar predatory behavior, it introduced an unknown bias into my estimates of predation parameters. Future studies capable of assessing this potential source of bias would be valuable (see Appendix II).

Although I demonstrate that GPS cluster techniques can be expanded beyond Anderson and Lindzey's (2003) application to ungulates and used to identify other prey >8 kg killed and consumed by cougars wearing collars with a 3-hour fix rate, prey <8 kg (e.g., snowshoe hare) are likely underestimated by this technique. Such small prey are easily consumed by a cougar in one feeding session spanning <3 hours (K. Knopff, unpublished data), resulting in the lack of cluster creation. Moreover, small prey often are entirely consumed (K. Knopff, unpublished data) and little evidence of the predation event may be available, making the kill difficult to find even if a cluster is created. Neonatal deer might fall into this category if they are killed in the first few weeks of life. Increasing fix rates to detect a greater proportion of smaller prey is possible (Webb et al. 2008), but creation of additional clusters to be visited in the field may be prohibitively labor intensive.

An important finding of my study is that monitoring periods must be long if accurate and precise estimates of cougar kill rate and prey composition are required (Figure 2.2). Because handling time, search time, and species killed are all variable, and because cougar predatory events occur infrequently, long monitoring periods are required to accumulate a sufficient number of inter-kill intervals and prey types to encompass this variation. For a cougar with a known 180-day kill rate of 0.7 prey >8 kg/week and a prey composition consisting of 72.2% deer, for instance, 36-day sub-sampling yielded kill rates between 0.38 and 1.55 prey >8 kg/week and a diet of between 25% and 100% deer. Consequently, prey selection or kill rate estimates derived from large carnivore sample units (i.e., individuals or groups) monitored for short periods could lead to inappropriate conclusions about predator-prey dynamics and about differences in predatory behavior (e.g., between regions, seasons, time periods, or age-sex classes). Most studies of large carnivore predation to date have not addressed this potentially important issue. The duration of monitoring required for quality parameter estimation will depend on the variability and average length of inter-kill intervals and on dietary diversity. Predators with shorter or less variable inter-kill intervals and lower dietary diversity will require shorter monitoring periods.

Where models can be employed for parameter estimation, they may greatly reduce cost and effort associated with monitoring over the duration necessary to generate quality estimates. *K*-fold validation of my top logistic regression model supports the assertion of Anderson and Lindzey (2003) that such models can be used effectively to predict cougar kill rates. My best model, however, proved to be quite different from the univariate number of nights at a cluster model adopted by Anderson and Lindzey (2003). Because cougars in my study displayed high fidelity to kill locations, commonly produced non-kill (bed-site) clusters at night, and occasionally produced clusters at predation events with only diurnal locations associated with them, I used the number of 24-hr periods to approximate Anderson and Lindzey's (2003) number of nights model. This univariate model, however, did not perform well when compared with other models in my candidate set (AIC wt = 0.00). My much larger sample size, inclusion of non-ungulate prey, and incorporation of a wider variety of explanatory variables may account for the difference in performance between studies. In addition, cougars in west central Alberta did not consistently use day beds >200 m from the kill as they did in Wyoming (Anderson and Lindzey 2003) and in California (Beier et al. 1995). In regions where remote day beds are common, a covariate or interaction term incorporating the proportion of nocturnal fixes at a cluster may be an important addition to my model. Although I suspect that my more comprehensive top model might improve on Anderson and Lindzey's (2003) univariate model outside my study area, I caution against its unguarded application. External validation using a representative sample of age-sex classes of cougars from several study areas will be required to fully assess the model's broader applicability. Such broad-scale meta-analyses should be possible in the near future given the prevalence of GPS collar use in contemporary studies of cougar ecology.

An essential caveat for the predictive success of my logistic regression models was the appropriate selection of the probability cutoff used to distinguish kills from non-kills (Table 2.3). A probability cutoff of 0.5 is automatically applied by most statistical software packages, and there may be some statistical benefits associated with its use (Hosmer and Lemeshow 2000). However, if prediction is the primary goal, cutoff selection using sensitivity-specificity analysis is preferred (Hosmer and Lemeshow 2000). Use of a 0.5 cutoff in the wolf kill rate model of Zimmermann et al. (2007), therefore, may have resulted in the inappropriate conclusion that the model was of little predictive value. I would have concluded similarly if I applied only a 0.5 cutoff when evaluating my top kill model (Table 2.3).

Using a sensitivity-specificity defined optimum, on the other hand, led me to conclude that the logistic model could be usefully applied for kill rate prediction. However, it is important to highlight that despite an outstanding discrimination between kills and non-kills obtained from ROC scores at the optimal cutoff using on all the data, k-fold analysis (withholding data for testing and allowing parameter coefficients to vary based on the remaining data) revealed that the ability of the model to predict kill rates within 10% of the true values occurs because false positives and false negatives cancel well at certain cutoffs, not because of near perfect discrimination between kills and non-kills (Table 2.3). This should be viewed as a red flag, indicating that caution is warranted when applying logistic models to predict kill rate without field visitation.

Moreover, because false positives and false negatives occur at different frequencies as cutoff level varies (Table 2.3), the blind application of sensitivity-specificity defined optimal cutoffs for all applications of the model should be avoided (Fielding and Bell 1997). Estimating the spatial distribution of predation risk, for instance, requires that kill locations are identified on a landscape and related to habitat characteristics (e.g., Hebblewhite et al. 2005, Kauffman et al. 2007). Using the optimal cutoff of 0.22 to identify kill locations would result in the incorporation of many non-kill locations (false positives) into the sample, resulting in substantial model contamination, which could be reduced by selecting a more conservative cutoff (e.g., 0.5 or higher). Conversely, when using the logistic model to improve field efficiency by eliminating some non-kill clusters from the visited sample while retaining most kills, a cutoff well below the optimum should be employed. The appropriate probability cutoff level, therefore, must be selected for each intended application of the logistic model.

Unfortunately, the multinomial models I used to predict cougar prey composition were not nearly as useful. The reasonable classification success I experienced was an artifact of the large number of deer in the sample and the propensity for the model to predict deer. Webb et al. (2008) obtained an equivalent result when using multinomial models to separate rare events (large or small prey) from each other and from a common event (no prey) at wolf GPS telemetry clusters. Webb et al. (2008) reported high overall model classification success (88%), but the ability to predict rare events (kills) was poor and the model misclassified 82% of small prey and 40% of large prey as non-kills. Precise estimates of prey composition are critical for certain management and conservation scenarios; e.g., identifying disproportionate population level prey selection which can lead to asymmetrical apparent competition (Chaneton and Bonsall 2000, Cooley et al. 2008) or detecting predators specializing in small populations of alternate prey (Knopff and Boyce 2007). For such applications, the under-representation of non-deer prey in my model predictions is unacceptable. The failure of multinomial models to effectively predict cougar prey species composition in west-central Alberta does not, however, preclude the use of such models to predict prey composition for other predators or for cougars in other places, especially where prey exhibit strong spatial segregation.

MANAGEMENT IMPLICATIONS

Studies of cougar predatory behavior conducted prior to the advent of GPS collar technology were constrained by available sampling techniques, resulting in estimates of behavioral parameters of predation that were generally derived from small sample sizes and short monitoring periods. Thus, the scope of appropriate inference and hypothesis testing regarding cougar predation has been limited. Global Positioning System telemetry cluster techniques offer a substantial improvement in efficiency for estimating these parameters, allowing detailed monitoring of predation histories over long periods for large numbers of cougars simultaneously. Although I found that I could estimate cougar kill rate using models alone, field visitation yields far better data and is a superior alternative when resources permit. I therefore recommend that researchers and managers wishing to understand and quantify the effects cougars have on populations of prey use appropriate logistic model probability cutoffs to direct field visitation when estimating parameter values. Field visitation is especially crucial in multi-prey systems where apparent competition or individual cougar specialization is suspected and their identification is important for effective management of ungulate populations. Proper application of GPS cluster techniques over monitoring periods of sufficient duration will promptly remedy the current paucity of detailed predation histories for individual cougars, improving the quality of parameter estimates and providing opportunities to enhance hypothesis testing and perhaps to resolve some of the controversy surrounding the effects cougars and other large carnivores have on their prey.

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CHAPTER 3

SCAVENGING MAKES COUGARS SUSCEPTIBLE TO SNARING AT WOLF BAIT STATIONS

Indiscriminate harvesting techniques capable of capturing both target and non-target species are commonly employed in the commercial, recreational, and subsistence harvest of fish and wildlife. Non-target harvest is especially common in fisheries, where efficient and economical harvests tend also to be indiscriminate (Jefferson and Curry 1994, Dayton et al. 1995, Stevens et al. 2000). Although less common in terrestrial systems, potentially indiscriminate harvest techniques in the form of traps and snares are occasionally employed (Phillips 1996, Shivik and Gruver 2002), and the ramifications of non-target harvest as a consequence of their use can be significant. In a study of efficacy of neck snares for predator control in Texas, for instance, Guthery and Beasom (1978) reported nearly as many non-target as target captures, and snaring was sufficient to cause unintentional extirpation of a local herd of collared peccaries (*Pecari tajacu*). In Africa, snaring targets a wide variety of species for the bush-meat trade and for subsistence (Noss 1998), but the lack of prey selectivity associated with snaring means that species that might otherwise be avoided (e.g., rare species of conservation concern but little economic value) are killed in snares meant to capture more profitable species (Rowcliffe et al. 2003).

In Alberta, Canada, cougars (*Puma concolor*) can be harvested legally by hunting, but they may not be trapped or snared. However, neck snares placed near carrion bait are often used to harvest wolves (*Canis lupus*) for management, recreation, and commercial purposes, and cougars, which are sympatric with wolves along the eastern slopes of Alberta's Rocky Mountains, are occasionally caught incidentally. Cougars killed by trappers may not be kept or sold, but are forfeit to the province (Alberta Fish and Wildlife 2008). Snaring mortalities thus detract from "optimum allocation of the cougar resource amongst recreational, commercial and other users," a primary goal of Alberta's cougar management plan (Jalkotzy et al. 1992:65). Accordingly, incidental cougar snaring is undesirable for both trappers and wildlife managers. The degree to which cougars are susceptible to capture at wolf bait stations, and the broader impacts of snaring on cougar population dynamics and its implications for cougar harvest management, however, have not been assessed.

Carrion bait provides a strong attractant for scavenging carnivores, and the inclination to scavenge determines susceptibility to capture in snares near bait. The propensity for wolves to scavenge has been well documented and makes them vulnerable to harvest at bait stations established by trappers (Huggard 1993, Hayes et al. 2000, Jedrzejewski et al. 2002, Stahler et al. 2006, Webb 2009). The evidence regarding the cougar's penchant for carrion is less clear. Most studies of cougar foraging indicate or assume that scavenging is rare, suggesting that susceptibility to snaring via attraction to baits should be low (Hornocker 1970, Ross and Jalkotzy 1996, Murphy 1998, Anderson and Lindzey 2003, Laundré 2008). Indeed, in a study of scavenger use of hunter and wolf-killed carcasses in the Greater Yellowstone Ecosystem, all large and medium-sized carnivores present, except cougars, were observed scavenging (Wilmers et al. 2003). However, carcasses left out as bait in California were frequently scavenged by cougars, and a report of a cougar in Oregon consuming only carrion for >3 weeks suggests that scavenging might play an important role in the diets of some cougars (Nowak et al. 2000, Bauer et al. 2005). Studies that focus on measuring the prevalence of scavenging behavior among individuals, the frequency with which individuals scavenge, and the dietary importance of scavenging are needed to clarify the role scavenging plays in cougar foraging ecology.

I studied foraging behavior, survival, and cause-specific mortality of cougars in west-central Alberta where snaring for wolves is prevalent. My primary objectives were to establish the role of scavenging in cougar foraging ecology, assess susceptibility to snaring at wolf bait stations, and evaluate the implications of this source of mortality for cougar population dynamics and harvest management. I hypothesized that cougars, like most vertebrate predators, would prove to be facultative scavengers (i.e., exploiting carrion opportunistically when encountered; DeVault et al. 2003, Selva et al. 2005). Specifically, I made the following predictions that conform to the principles of the facultative scavenger hypothesis (DeVault et al. 2003). First, scavenging would be a common foraging strategy at the population level (i.e., most individuals would scavenge). Second, scavenging rates would increase as carrion availability increased and carrion would constitute an important component of the diet where it was abundant and accessible to cougars (i.e., cougars would not pass up a free lunch). Third, scavenging would be incorporated into the foraging strategies of healthy cougars and not simply used as a last resort by energetically compromised animals that were forced to scavenge to survive. If these predictions held, I further expected cougars to be attracted to wolf bait stations and hence susceptible to snaring.

STUDY AREA

My study area consisted of 16,900km^2 of mountains, foothills, and agricultural lands located just east of Banff and Jasper National Parks in western Alberta, Canada (centered approx. at 52°18'N, 115°48'W). The region's climate over the course of my study was characterized by wet springs, warm dry summers, and cold snowy winters. Warm dry winds from the west (known locally as chinooks) periodically eliminated the snow-pack from south-facing slopes. Conifer forests composed primarily of lodgepole pine (*Pinus contorta)* and white spruce (*Picea glauca*) dominated the study area. Both forestry and oil and gas industries were active on the landscape, creating networks of roads, seismic lines, well sites, and clear-cuts. Snaring for wolves was permitted on public lands in the study area between 1 December and 31 March under Alberta's Registered Fur Management Area (RFMA) program (Alberta Fish and Wildlife 2008). The study area contained 66 RFMAs, but a recent survey of trappers in the area indicates that only about 56% of those holding RFMAs actively trapped for wolves (Webb et al. 2008). Trappers who pursued wolves usually had ≥1 wolf bait station on their RFMA each year. Wolf bait stations consisted of carrion bait (most often >1 ungulate carcass plus occasional scraps and small mammal remains) and 20–60 snares set within a few-hundred-meter radius. Trappers usually replenished baits regularly during the season. Wolves were trapped most actively in December–February, when pelts were prime, and much less actively in March when pelts were rubbed and had lower value (Barrus et al. 1997).

Big game hunting also was popular in the region and licensed ungulate harvest occurred in the fall (Aug–Dec). Treaty Indians were exempt from normal hunting regulations but harvested animals most frequently in fall and winter (Aug–Mar). Both licensed and unlicensed hunters regularly left gut-piles, bones, and hide in the field, providing opportunities for scavengers. Carrion derived from human activities therefore was more abundant in fall and winter than in summer. Other scavenging opportunities for cougars were created, year round, by vehicle-wildlife collisions on roads, by predatory activities of other carnivores (e.g., wolves), and at domestic animal carcass dumps on agricultural lands. Cougars were managed as a big-game animal and were hunted according to a quota system with seasons running from 1 December–28 February or until the quota filled (Ross et al. 1996). In addition, landowners were permitted to shoot cougars on their private land at any time of year.

METHODS

Capture and Monitoring

I captured 44 cougars, some more than once (totaling 57 captures), between December 2005 and May 2008 under the authority of a provincial research and collection license (no. 19872-CN) and an approved University of Alberta Animal Care Protocol (no. 479505). I used trained hounds to track and tree cougars and then chemically immobilized them by administering 3 mg/kg zolazepam-tiletamine (Telazol®, Fort Dodge Animal Health, Fort Dodge, IA) and 2 mg/kg xylazine (Rompun®, Bayer, Inc., Toronto, ON, Canada). Once immobilized, I weighed, measured, sexed, and aged cougars. I estimated age using a combination of tooth color and wear characteristics (Ashman et al. 1983, Shaw 1986), pelage spotting progression (Shaw 1986), and gum-line recession (Laundré et al. 2000). I assigned cougars to one of 3 age brackets: kitten (still with mother), sub-adult (dispersal, usually around 12-18 months to 2.5-3 yr), or adult (>2.5-3 yr). My sample of collared cougars included 23 adult females, 6 adult males, 6 sub-adult females, and 9 sub-adult males at capture. Three sub-adult females and 2 sub-adult males transitioned to adults during the study. On most capture occasions (*n* = 46), I fitted cougars with Lotek 4400s Global Positioning System (GPS) collars (Lotek Engineering, Newmarket, ON, Canada), but I also deployed 6 H.A.B.I.T GPS-very high frequency (VHF) collars (H.A.B.I.T research, Victoria, BC, Canada) and 5 Lotek VHF collars. At the completion of the handling procedure, I gave cougars 0.125mg/kg yohimbine

(Yobine®, Lloyd Laboratories, Shenandoah, IA) to reverse effects of xylazine, and I released them.

All collars deployed on cougars were equipped with mortality sensors which caused the VHF pulse rate to double if the collar was immobile for >18 hours, facilitating identification of mortality events. I monitored collared cougars intensively between December 2005 and August 2008 using a combination of ground and aerial VHF telemetry (I attempted ≥1 relocation/cougar/week). In addition, I programmed GPS collars to obtain a location fix every 3 hours and I downloaded these data from the ground and occasionally from the air every 2-3 weeks. I investigated mortality signals as soon as possible after I detected them and assigned date of death using the first GPS location at the mortality site. When cougars were killed by hunters, I assigned date of death using information provided by the hunter and confirmed by the last GPS location fix in the cougar's home range.

Scavenging Behavior

I used a rule-based algorithm to identify clusters of location fixes from GPS data and then systematically searched clusters in the field for evidence of predation and scavenging events (Chapter 2). Prior to November 2007 I visited nearly all clusters of ≥2 locations occurring within 200 m of each other and within a temporal window of 6 days. From November 2007 to August 2008 I used a logistic regression model to screen clusters with a near zero probability of a kill site from the set I visited in the field. If the model estimated a probability of a kill <0.15 in winter (defined here as 15 Oct-14 Apr) or <0.1 in summer (15 Apr-14 Oct) I did not visit the cluster. Specific details of cluster visitation techniques and models used to guide field efforts are described in Chapter 2. I visited clusters of each collared cougar for as long as the collar continued to function. Although cluster visitation was my primary means of data collection accounting for most of the cougar foraging events I located, I also occasionally snowtracked collared and uncollared cougars to identify predation or scavenging events.

I classified feeding on a carcass as a scavenging event only if there was clear evidence that the animal had been killed by something other than the focal cougar. Evidence for scavenging included: 1) identification of an animal that had clearly died before the date that the collared cougar visited the site, 2) evidence that the carcass was of an animal that had been wounded or killed by a hunter (arrow or bullet wound), 3) evidence that the carcass had been dumped by humans (trapper bait station, livestock dump site, knife or saw marks on bones of wild ungulates), 4) broken bones and carcass proximity to a road that would indicate a collision with a vehicle, or 5) evidence that the animal had been killed by another predator.

Once I determined that carrion had been scavenged by a cougar, I identified the species and age-sex class of the carcass. I also estimated the type of foraging opportunity the carcass presented to the cougar (e.g., whole animal or any combination of meat, hide, or bone) by carefully investigating the carcass remains and by examining cougar scat associated with the cluster. Global Positioning System data allowed me to estimate the amount of time cougars spent accessing foraging locations, delineating handling time for 73 scavenging events and 1,254 predation events. Cougar handling time was significantly and positively related to prey size (i.e., available biomass) at predation events in west-central Alberta (Chapter 4), leading me to assume that handling times can be used to approximate the energetic value of a foraging opportunity. I used a single-factor analysis of variance (ANOVA) followed by non-orthogonal planned comparisons, evaluated using the Dunn-Sidàk method (Day and Quinn 1989), to compare handling times among 4 classes of scavenging events: 1) kills made by other carnivores, 2) hunter carcasses, 3) trapper bait stations, and 4) all other scavenging events.

I calculated scavenging rates for each GPS-collared cougar separately for summer and winter. Because short monitoring periods might not provide a representative sample of feeding behavior, I used data only from cougars with ≥28 days of continuous monitoring in a given season (Chapter 2). I calculated scavenging rates in 2 ways. First, I simply divided the number of scavenging events I observed during a seasonal monitoring period by total number of days monitored (Hebblewhite et al. 2003), which gave a measure of frequency but no measure of the relative energetic importance of scavenging for each cougar. I therefore also divided handling time at scavenging events by number of days monitored to obtain a rate (hr/day) that measured the amount of time different cougars invested in scavenging.

A prediction of the facultative scavenging hypothesis is that cougars will scavenge more frequently when carrion is more abundant. In my study area, humans deposited carrion on the landscape more commonly in winter during the trapping and hunting seasons than in summer. Although I did not directly estimate the biomass of carrion provided by hunters and trappers, other studies in similar systems have shown that it can be substantial (Wilmers et al. 2003). Winter-killed ungulates and slow carcass decomposition in cold weather also increase carrion availability in winter. Consequently, I predicted that cougars would scavenge more often during winter (15 Oct–14 Apr). I tested this prediction using a one-tailed paired t-test for individual cougars for which I was able to calculate a scavenging rate in both summer and winter. Differences in hunting efficiency and energetic needs among cougar age-sex classes also may influence scavenging behavior. I therefore compared scavenging rates between adult males, adult females, and sub-adults and used a two-tailed t-test to determine whether adult and sub-adult animals scavenged at significantly different rates ($P < 0.05$).

Survival and Cause-Specific Mortality

Like many species of harvested wildlife (e.g., Hasbrouck et al. 1992), cougars do not experience constant survival throughout the year, but exhibit a strong mortality pulse associated with the hunting season (Ross and Jalkotzy 1992, Lambert et al. 2006). For populations with identifiable mortality pulses such as these, a modification of the binomial Mayfield (1975) estimator by Heisey and Fuller (1985) using defined mortality periods may be the most appropriate technique for simultaneously estimating annual survival and cause-specific mortality (Heisey and Patterson 2006, Murray 2006). However, this method assumes constant mortality risk within periods, violations of which can result in poor survival estimates (Tsai et al. 1999). Alternative estimators are Kaplan-Meier (Pollock et al. 1989) for survival and Heisey-Patterson (Heisey and Patterson 2006) for cause-specific mortality. These estimators make no assumptions about constant mortality but are sensitive to the sample size of radiomarked animals on days where mortalities occur (i.e., animals collared on a given day are assumed to be representative of the population), and cause-specific mortality estimated this way can have unacceptably high variance or even be undefined (Heisey and Patterson 2006).

The Heisey-Fuller method reduces to the Kaplan-Meier survival estimator and the Heisey-Patterson cause-specific mortality estimator when the mortality period is defined to be a day (Heisey and Patterson 2006), making it easy to calculate survival and mortality estimates using different approaches. Therefore, following Heisey and Fuller (1985), I calculated daily survival rates (s_i) using

$$s_i = \frac{x_i - y_i}{x_i} \qquad \text{(Equation 3.1)}$$

where x_i is number of radiodays during the i^{th} monitoring period and y_i is number of mortalities during that same period. I calculated annual survival (S^*) using

$$S^* = \prod_{i=1}^{n} (s_i^{L_i}) \qquad \text{(Equation 3.2)}$$

where L_i is number of days in the i^{th} monitoring period and the duration of all monitoring periods sum to 365 days. Finally, I calculated cause specific mortality (M_j^*) using

$$M_j^* = \sum_{i=1}^{n} \left(\left(\frac{m_{ij}}{1 - s_i} \right) \left(1 - s_i^{L_i}\right) \right) \prod_{i=0}^{n-1} s_i^{L_i} \qquad \text{(Equation 3.3)}$$

where $s_0 = 1$ and $m_{ij} = y_{ij} / x_i$ where y_{ij} is number of deaths caused by mortality source j during monitoring period i. I calculated variance and 95% confidence intervals around S^* and M_j^* by bootstrapping the estimate using 10,000 re-sampling iterations where I randomly selected with replacement individual cougars from my original sample for each iteration. I calculated S^* and M_j^* for the cougar population as a whole and for males and females separately.

When applying the Heisey-Fuller approach to populations with clear mortality pulses, mortality periods (i) should be chosen in such a way that probability of death varies between periods but remains constant within them. Heisey and Fuller (1985) recommend using the least number of periods possible for the sake of parsimony. I therefore divided the year into 2 periods, a high-mortality period (1 Dec-28 Feb, which encompassed the entire cougar hunting season and the most active part of the wolf snaring season) and a low-mortality period (1 Mar-30 Nov). I also estimated survival and cause-specific mortality using day as the mortality period in equations 3.2 and 3.3 (i.e., Kaplan-Meier and Heisey-Patterson). The different techniques should yield similar results provided their respective assumptions are met and sample sizes are sufficiently large (Heisey and Patterson 2006, Murray 2006). Substantial deviations would indicate that assumptions of ≥1 methods were violated and would require further scrutiny.

All human-caused cougar mortalities in Alberta must, by law, be registered with the provincial government. I used these registered mortality incidents to assess temporal variation in mortality patterns between 1990 and 2008 in the provincial Wildlife Management Units (WMUs) that partially or completely overlapped my study area (i.e., Alberta's WMUs 318, 320, 322, 324, 326, 328, 330, 417, 418, 420, 422, 426, 428, 429, 430, 432, and 434). I also obtained annual wolf harvest data from all RFMAs in my study area and correlated these data with the proportion of human-caused cougar mortality due to snaring to test the assumption that the relative importance of snaring as a cause of cougar mortality would be related to trapper effort and success at wolf snaring in a given year. Because both cougar hunting and wolf snaring seasons begin 1 December, I treated that date as the start of a new year for grouping mortality data.

RESULTS

Monitoring yielded 12,080 cougar radiodays and 47,998 GPS locations. I visited 3,407 cougar GPS location clusters (1,776 in summer and 1,629 in winter) and also tracked VHF collared and uncollared cougars through the snow in winter, amassing >400 km of snowtracking data. I located 1,455 cougar feeding events (on average 25.7 days after the first GPS location at a cluster, SD = 23) and classified 83 of these as scavenging. I calculated 42 winter and 33 summer scavenging rates (I calculated rates once in each age class for individuals that transitioned to an older age class during the study). Most individual cougars (64%) scavenged at least once. I excluded 4 cougars from scavenging rate analyses because their foraging behavior was affected by collaring (Appendix II) and I excluded one cougar because his collar failed before I accumulated 28 days of continuous monitoring.

Cougars of all age-sex classes scavenged but subadults did so most often (0.144 events/week, SD = 0.17, *n* = 13), followed by adult females (0.043 events/week, SD = 0.097, *n* = 22) and adult males (0.021 events/week, SD = 0.023 , *n* = 7). On average, sub-adults scavenged approximately 4 times more frequently than adults (t_{40} = 2.7, *P* = 0.01). Cougars also scavenged 4 times more frequently in winter (0.13 events/week) than in summer (0.03 events/week; t_{29} = 2.09, *P* = 0.02). Amount of time cougars spent at scavenging events tended to be longer in winter ($\bar{x}$ = 59.3 hr, SD = 70.0, *n* = 55) than in summer ($\bar{x}$ = 31.0 hr, SD = 32.1, *n* = 18), but this difference was not significant (t_{71} = 1.65, *P* = 0.10). Frequency of scavenging events varied by month and scavenging was most common in February–April (Figure 3.1).

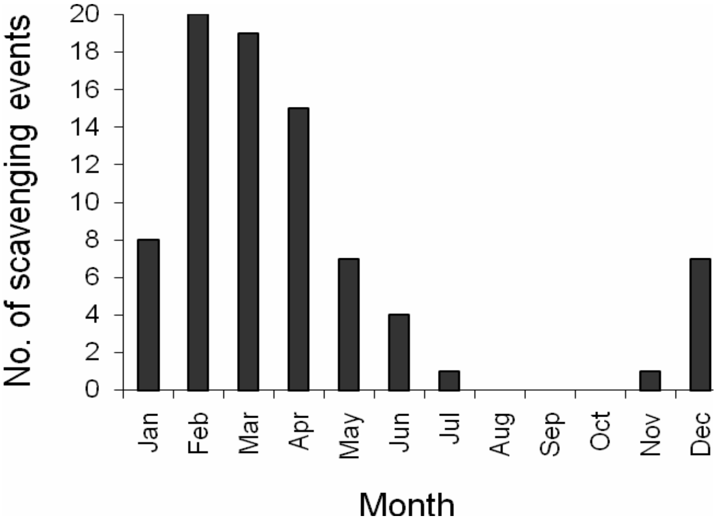

Figure 3.1: Number of cougar scavenging events identified at Global Positioning System (GPS) telemetry clusters in each month in west-central Alberta, Canada, during 2005–2008.

Cougars cached kills by covering carcasses with woody debris, grass, or snow between feeding events, and I noted that this behavior was also common at scavenging locations, provided there was sufficient carrion available to permit multiple feedings. Of the 83 carcasses scavenged by cougars most were at trapper bait stations (29%), followed by hunter-killed animals (23%), and aniumals killed by other carnivores (14%). A single-factor ANOVA showed that scavenging sources differed in handling time ($F_{3,69} = 6.49$, $P < 0.001$; Figure 3.2) and Dunn-Sidàk tests revealed that this difference was driven by higher handling times at bait stations. Although unequal variance and substantial difference in sample size did not permit statistical comparisons between handling time at different scavenging types and predation events (Day and Quinn 1989), mean time spent at bait stations also was longer than time spent at predation events (Figure 3.2). Bait stations where cougars fed often included >1 entire ungulate carcass plus meat scraps and small mammal carcasses, whereas predation normally resulted in one ungulate prey, and carcasses left by other carnivores or hunters typically consisted of only portions of an ungulate. Handling times therefore match the available biomass of the various foraging types (Figure 3.2).

Some cougars spent substantial time feeding on carrion. For example, 5 cougars spent >35% of their total handling time during winter scavenging (2 of these were sub-adult females that spent close to 50% of their handling time consuming carrion). Moreover, scavenging is not a strategy employed only by cougars that have depleted energy reserves and so must scavenge to survive. Healthy cougars with demonstrated killing ability also scavenged frequently and so were susceptible to snaring (Figure 3.3).

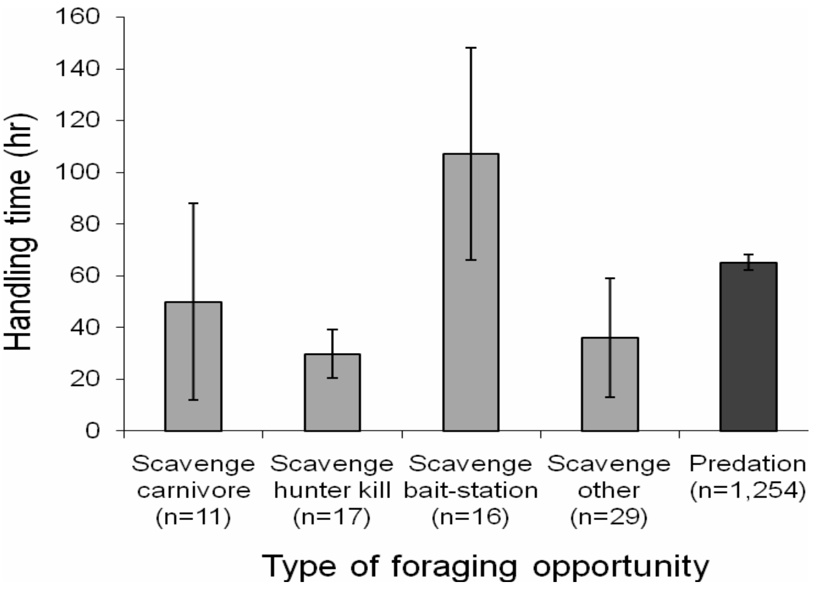

Figure 3.2: Mean handling time of cougars feeding at scavenging locations classed by carcass source and at predation locations (shown with 95% CI) in west-central Alberta, Canada, during 2005–2008.

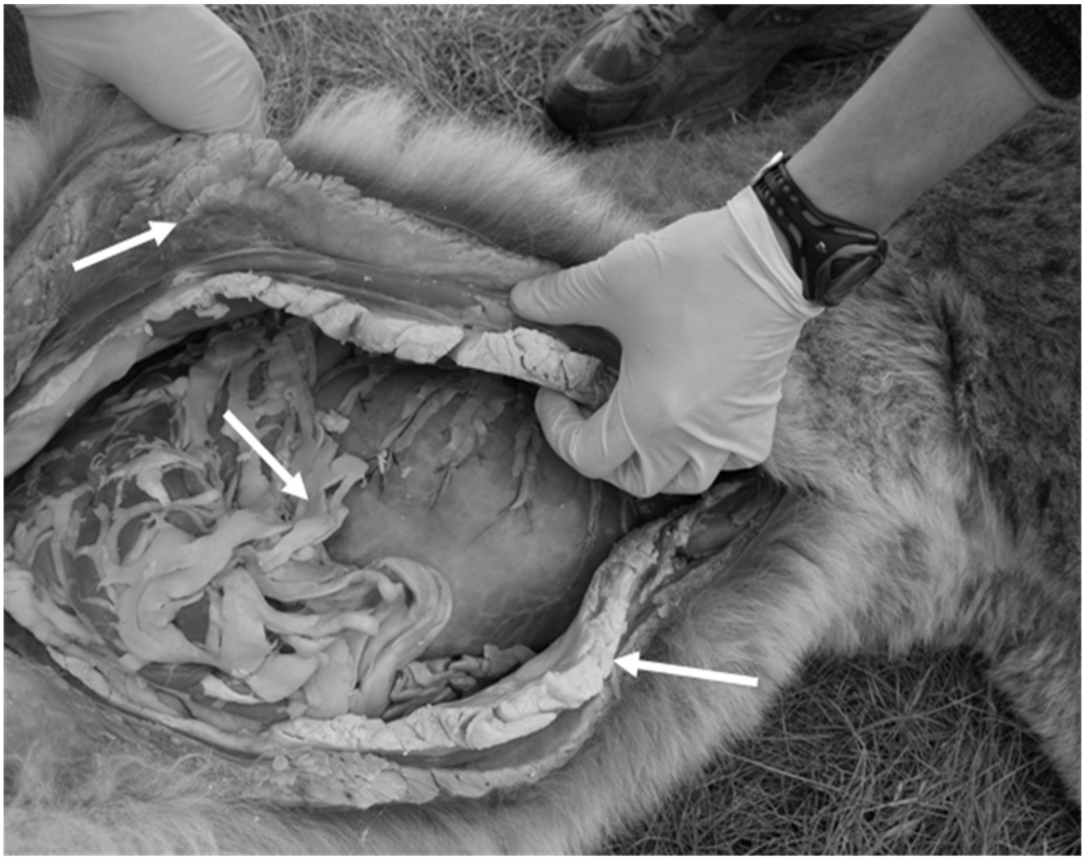

Figure 3.3: Heavy deposition of subcutaneous and visceral fat revealed during the field necropsy of an adult female cougar snared at a wolf bait station in west-central Alberta, Canada, in 2008. Fat stores on this cougar, which spent 20% of its foraging time scavenging over the 80 days it wore a Global Positioning System [GPS] collar, suggests that carrion can be incorporated into successful foraging strategies employed by healthy cougars.

I recorded 16 mortalities of radiocollared cougars during my study. I excluded 4 of these cougars from inferences of population-level survival and cause-specific mortality because their deaths were attributed to delayed effects of capture and collaring and hence were not considered representative (Appendix II). Cougars were susceptible to snaring at wolf bait stations and 33.3% ($n = 4$) of mortalities were a result of snaring. Other mortality sources were licensed hunting ($n = 6$), poaching ($n = 1$), and landowner harvest ($n = 1$). Thus, 100% of radiocollared cougar mortality during my study was human-caused.

I calculated survival and cause-specific mortality using a sample of 40 cougars (11,907 radiodays). I combined poaching, hunting, and landowner harvest together into one cause-specific category (shooting), and snaring made up the other category. All mortalities of radiocollared cougars occurred during the high mortality period (1 Dec–28 Feb) resulting in a cumulative daily mortality hazard of 0 for much of the year, with a rapid increase in hazard beginning 1 December (Figure 3.4). I calculated an annual survival of 0.67 using the Heisey-Fuller approach with 2 mortality periods (Table 3.1) and 0.68 when I used day as the mortality period (i.e., Kaplan-Meier), indicating that the assumption of constant mortality during the high harvest season was met by my data. Likewise, Heisey-Fuller estimates of cause-specific mortality (snaring = 0.11, shooting = 0.22) were similar to those estimated using Heisey-Patterson (snaring = 0.12, shooting = 0.20). For the sake of brevity and consistency, all other results are given only using Heisey-Fuller estimates (Table 3.1). There was a non-significant tendency for males to have lower annual survival than females (Table 3.1). However, while males tended to have a higher annual probability of being killed by a hunter, females were more likely to be snared (Table 3.1).

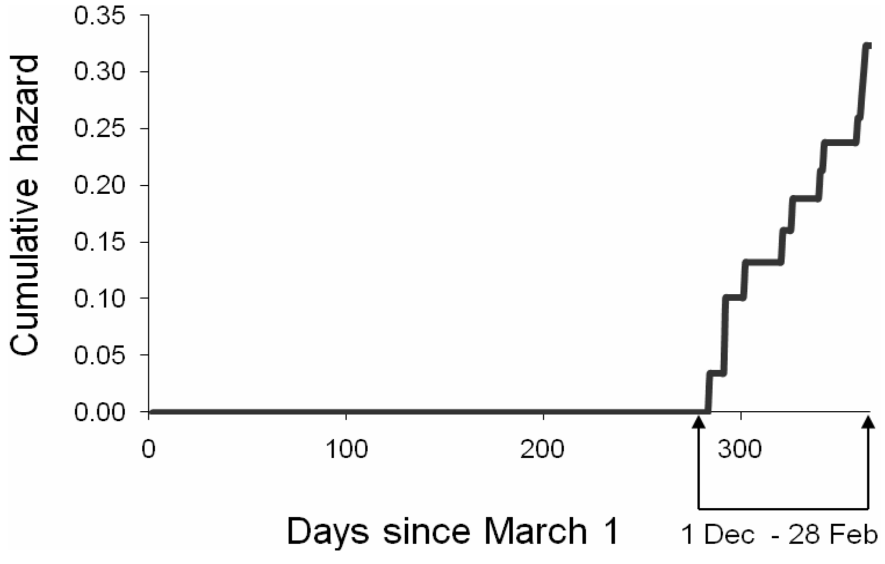

Figure 3.4: Cumulative annual mortality hazard (proportion of the population expected to die) calculated using 1 minus the Heisey-Fuller survival estimate (equation 2 where day was the monitoring period) for 40 radiocollared cougars in west-central Alberta, Canada, during 2005–2008.

Provincial records were consistent with my radiotelemetry results. Most of the 579 human-caused mortalities (94%) reported to the province in my study area during 1991–2008 occurred during the cougar-hunting season and active portion of the wolf-trapping season (i.e., 1 Dec–28 Feb). Hunting was the most important source of human-caused mortality, but up to 27% of annual registrations resulted from incidental snaring (Figure 3.5). Most cougars (60%) taken incidentally by trappers were female. These consistencies were evident even though registered mortalities can underestimate the importance of snaring if trappers fail to report snaring incidents or if cougars break snares and die away from the bait station, leaving the trapper with nothing to report. One of the radiocollared cougars I monitored, for instance, broke the snare below the lock, escaping the bait station only to have the snare eventually kill her. In a second case, I captured a cougar that had a snare (broken at the lock and unable to tighten) attached to her neck, indicating that breaking snares may not be uncommon (Figure 3.5). Thus, snaring might be a more important source of mortality than provincial records indicate.

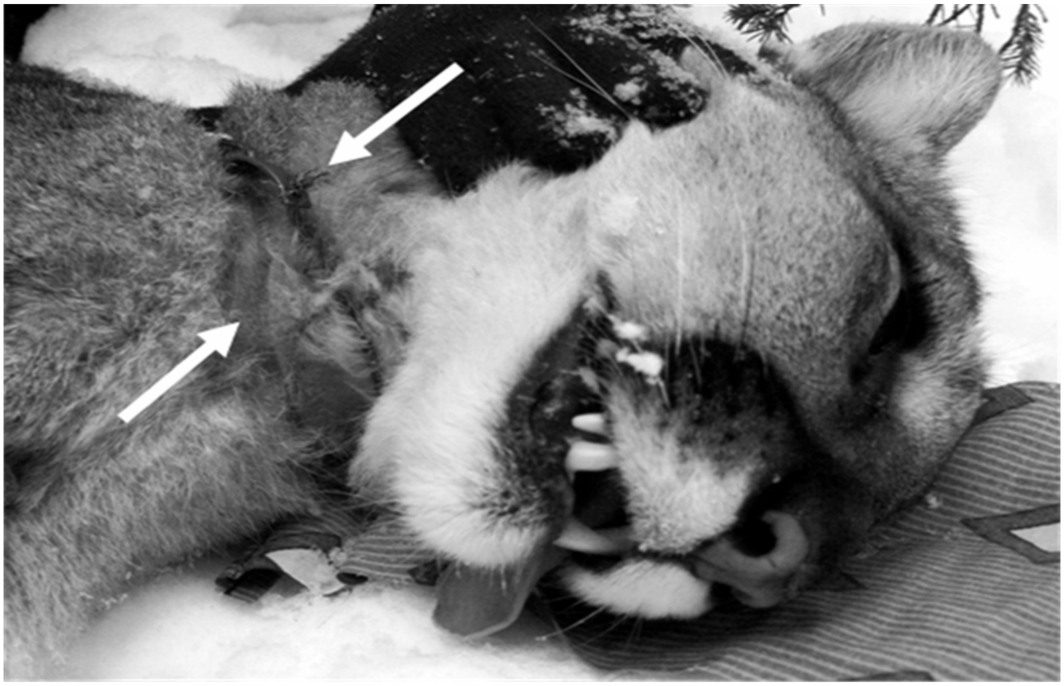

Figure 3.5: An anesthetized adult female cougar in west-central Alberta in 2008 with a broken snare attached to her neck. Note the extensive scarring below the snare. Although this cougar survived, the incident highlights the potential for cougars to break snares, which might bias provincial data such that the importance of snaring as a mortality source is underestimated.

Table 3.1: Survival and cause specific mortality of 40 radiocollared cougars calculated using the Heisey-Fuller method with 2 mortality periods in west-central Alberta, Canada, during 2005–2008. Results are given at the population level and for males and females separately.

		Mar-Nov		**Dec-Feb**		**Annual**	
		Rate	**95% CI**	**Rate**	**95% CI**	**Rate**	**95% CI**
Survival	**Population**	1.00	1.00-1.00	0.67	0.53-0.81	0.67	0.53-0.81
	Male	1.00	1.00-1.00	0.60	0.38-0.84	0.60	0.38-0.84
	Female	1.00	1.00-1.00	0.70	0.53-0.87	0.70	0.53-0.87
Snaring mortality	**Population**	0.00	0.00-0.00	0.11	0.02-0.21	0.11	0.02-0.21
	Male	0.00	0.00-0.00	0.07	0.00-0.26	0.07	0.00-0.26
	Female	0.00	0.00-0.00	0.12	0.00-0.23	0.12	0.00-0.23
Shooting mortality	**Population**	0.00	0.00-0.00	0.22	0.09-0.35	0.22	0.09-0.35
	Male	0.00	0.00-0.00	0.32	0.08-0.59	0.32	0.08-0.59
	Female	0.00	0.00-0.00	0.17	0.04-0.32	0.17	0.04-0.32

Both hunting and snaring mortalities increased substantially over the past 2 decades, with total number of human-caused cougar deaths escalating by approximately 600% between 1991 and 2008 (Figure 3.6). Whereas snaring mortality is highly variable among years (Figure 3.6), the general trend nevertheless indicates that snaring has made up an increasingly important proportion of all human-caused mortality over time (increasing at 1.2%/year, $R^2 = 0.61$; Figure 3.7). This increase is mirrored by an increasing wolf harvest (increasing at 2.4 wolves/year, $R^2 = 0.43$; Figure 3.7), and I identified a positive correlation between number of wolves snared and annual proportion of human-caused cougar mortality due to snaring ($P = 0.04$, $R^2 = 0.27$, $n = 16$).

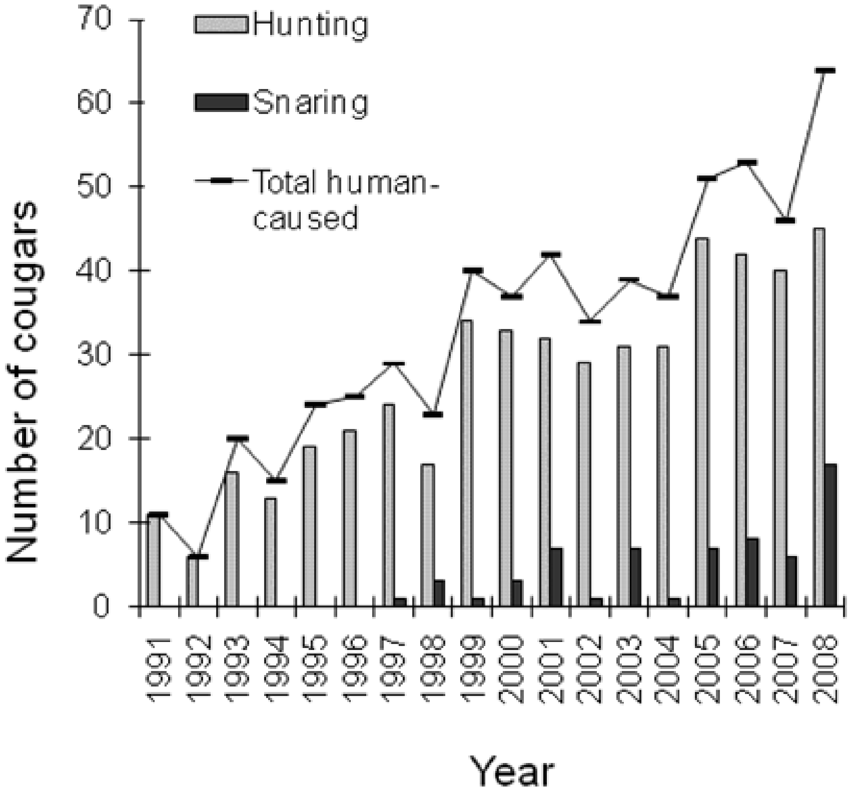

Figure 3.6: Number of cougars snared and hunted and total annual mortality of cougars reported through a mandatory provincial cougar registration program in west-central Alberta, Canada, during 1991–2008.

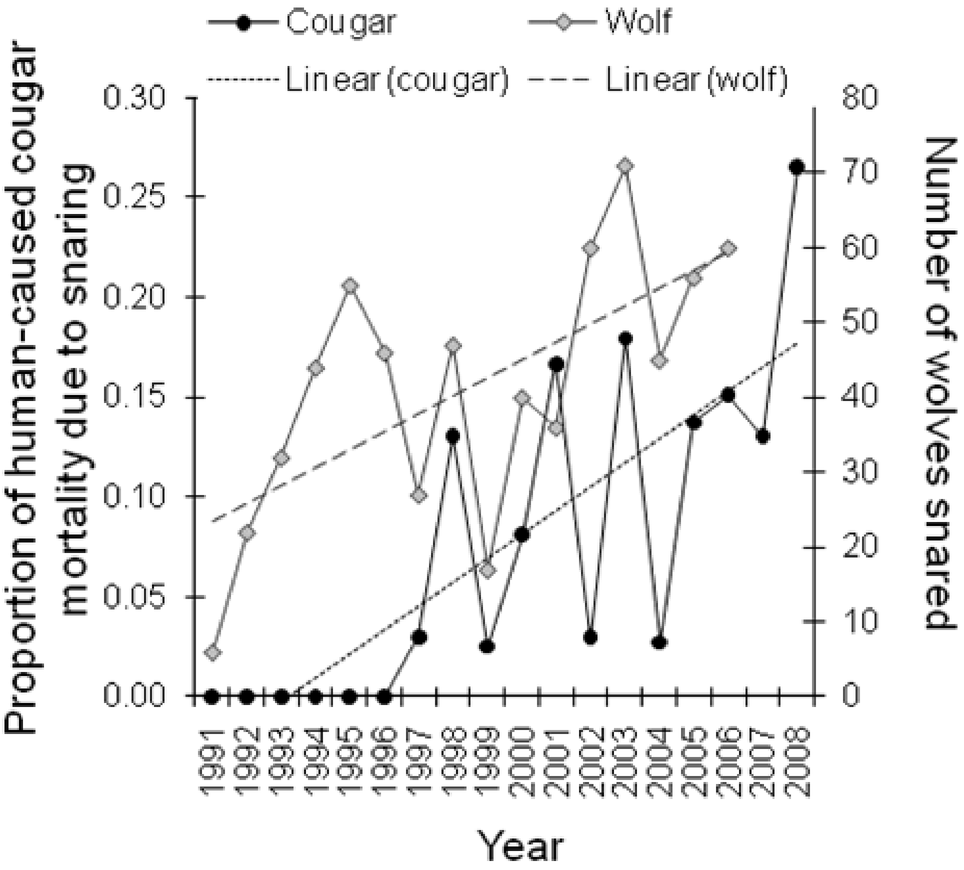

Figure 3.7: Proportion of total annual human-caused cougar mortality resulting from non-target snaring and total number of wolves snared annually as reported through mandatory provincial registration programs in west-central Alberta, Canada, during 1991–2008. The best-fit regressions against year are displayed for cougars (proportion of mortality due to snaring increasing at 0.012/yr) and for wolves (no. snared increasing at 2.4 wolves/yr).

DISCUSSION

Scavenging Behavior

My results support the hypothesis that cougars, like most predators, are naturally inclined to scavenge (DeVault et al. 2003, Bauer et al. 2005). Cougars in west-central Alberta conformed to all 3 predictions for facultative scavengers: 1) scavenging was a common foraging strategy employed by most cougars in the population, 2) scavenging increased during winter when carrion availability was higher and some cougars spent a substantial portion of their foraging time consuming carrion during winter, and 3) healthy adult cougars with demonstrated killing ability incorporated scavenging into their foraging strategy. Indeed, I probably underestimated the true importance of scavenging because GPS cluster visitation does not always detect feeding events where available biomass is low (Chapter 2), and some cougar scavenging opportunities might have involved carcasses with limited edible material.

Inclination for cougars to scavenge should not be surprising since scavenging allows cougars to take advantage of foraging opportunities while avoiding risks associated with predation (e.g., Ross et al. 1995, Logan and Sweanor 2001). Given this benefit, cougars might scavenge whenever edible carrion is encountered and has not been monopolized by a competitor. The reason that I observed higher scavenging rates for sub-adults might be because they are less-efficient predators (Murphy 1998; Chapter 4) and are forced to spend more time searching for food, increasing their encounter rate with carrion. Spoilage of animal carcasses in warm weather imposes costs because of possible toxicity that will eventually outweigh the benefits of scavenging, partially explaining the observed reduction in scavenging rates and tendency to shorter handling times in summer (DeVault et al. 2003, Bauer et al. 2005).

Scavenging in west-central Alberta also confirms the suspicions of Bauer et al. (2005) that misclassified scavenging events can influence kill rate estimation for cougars. Kill rate estimators that rely on telemetry data alone (e.g., Anderson and Lindzey 2003, Laundré 2008), delayed visitation of telemetry clusters (e.g., Anderson and Lindzey 2003), or energetics models (e.g., Laundré 2005) may overestimate the importance of predation. Indeed, using the logistic regression model and optimal probability cutoff proposed in Chapter 2 to calculate kill rate without field visitation would have inflated winter kill rate estimates by ≥25% for the 5 individual cougars that scavenged most frequently. Even when clusters are visited in the field, conservative estimates of scavenging rates (and overestimated kill rates) are possible because of the potential to misclassify as predation fresh carcasses that cannot be clearly identified as being killed by something other than a cougar.

Although scavenging was reported in some of the earliest studies of cougar diet (Young 1946), its importance has remained obscure, probably because scavenging rates have been difficult to estimate. Estimating foraging patterns via scat analysis, for instance, does not permit differentiation between predation and scavenging events (e.g., Rosas-Rosas et al. 2003), nor does visiting GPS location clusters if the delay between cluster creation and visitation is long (e.g., Anderson and Lindzey 2003). In such cases predation is often assumed. Indeed, failure to recognize the importance of scavenging is a common problem in studies of vertebrate predators, precisely because ecologists tend to focus their attention on predation (DeVault et al. 2003). Monitoring cougar foraging behavior using daily radiotelemetry and regular field checks of radiolocations allows researchers to identify scavenging events, but logistical challenges associated with these techniques tend to yield short monitoring periods and low sample sizes (Murphy 1998, Nowak 1999, Cooley et al. 2008). Downloadable GPS collars permitted me to visit large numbers of telemetry location clusters shortly after they were made, allowing me to circumvent many of these problems and calculate cougar scavenging rates for the first time. Similar techniques might be applied for estimating scavenging rates in other large carnivores.

Susceptibility to Snares and Harvest Management

The propensity for cougars to scavenge makes them vulnerable to snaring at bait stations, with important implications for cougar populations and harvest management. Eleven percent of the cougar population was removed annually as a result of incidental snaring alone, and my estimated annual human-caused mortality of 33% of independent cougars more than doubles the maximum annual human-caused mortality of 15% recommended in Alberta's cougar management plan (Jalkotzy et al. 1992). Although cougar populations are capable of rapid growth (Ross and Jalkotzy 1992, Logan and Sweanor 2001), annual harvest of 30-50% of independent cougars has been shown to cause populations to decline (Anderson and Lindzey 2005, Lambert et al. 2006, Stoner et al. 2006). This is especially true if, as I found in west-central Alberta, annual mortality of independent and potentially reproductive females exceed 20-25% (Anderson and Lindzey 2005, Lambert et al. 2006).

Although I did not measure it directly, survival of dependent kittens and juveniles also can be reduced in heavily harvested populations. Females traveling with spotted kittens cannot legally be hunted in Alberta, but mothers often travel independently and thus are susceptible to harvest (e.g., Barnhurst and Lindzey 1989, Anderson and Lindzey 2005, Laundré and Hernàndez 2008). In my study, 29% of harvested females (2/7, one hunter harvested, one snared) had dependent kittens <8 months old. Therefore, while I recognize that the confidence interval around my annual survival estimate is wide and that true survival of independent cougars near the upper 95% limit (0.81) is compatible with stable or even increasing populations, I point out that my data are more consistent with a declining or sink population (Anderson and Lindzey 2005, Stoner et al. 2006, Robinson et al. 2008).

During my study, hunting quotas were set in advance and were usually filled; hence, hunting mortality was fixed. Natural mortalities tend to be rare in heavily harvested cougar populations (Anderson and Lindzey 2005, Lambert et al. 2006, Robinson et al. 2008, but see Stoner et al. 2006), a pattern that is further supported by my results. Thus, managing the substantial and variable non-target mortality at wolf bait stations represents an important component of cougar population management in west-central Alberta. This is one of the first times population-level consequences for non-target animals killed unintentionally by indiscriminate harvest techniques have been identified in a terrestrial ecosystem.

Incidental cougar capture at wolf bait stations is a new management concern in west-central Alberta; cougar mortality due to snaring only became prevalent after 1997 and has increased steadily since. In part, the increase in the number of cougars snared might be a result of a growing provincial cougar population. Increasing cougar numbers across North America in recent decades is apparent in genetic evidence and the re-colonization of portions of cougar range east of the Rocky Mountains (Biek et al. 2006, Thompson and Jenks 2007, Bacon and Boyce 2009). Moreover, increased cougar harvest in western states and provinces is a response by management agencies to perceived growth in cougar populations. The approximately 600% growth in human-caused cougar mortality in west-central Alberta over the last 2 decades parallels similar patterns in other jurisdictions (e.g., Riley and Malecki 2001, Keister and Van Dyke 2002, Toweill et al. 2008). Density estimates based on intensive collaring efforts indicate that cougar populations as much as tripled in west-central Alberta during 1991-2006 (Appendix I), although high harvests reported in this study might have begun to curb or even reverse that trend.

The proportion of human caused mortality attributed to snaring also increased over time, and I found a significant positive relationship between the annual proportion of cougars dying in snares and the number of wolves snared, suggesting that changes in trapper effort might be driving changes in incidental cougar harvest. Increasing wolf numbers in west-central Alberta and attempts by provincial agencies to increase efficacy of snaring as a wolf management tool by sponsoring snaring courses and helping licensed trappers to obtain road-killed ungulates for bait may have resulted in higher trapper effort (Webb 2009; J. Allen, Alberta Sustainable Resource Development, personal communication). Although reducing the number of bait stations on the landscape should reduce incidental cougar captures, reducing harvest of target species such as wolves may not be a desirable outcome for managers in many situations. Under these circumstances, strategies for maintaining wolf harvest while reducing incidental cougar capture are necessary.

Overall, snaring remained more effective at targeting wolves than cougars on a per-capita basis. I report an annual snaring-specific mortality rate of 0.11 for cougars, and Webb (2009) found a rate of 0.26 for wolves in the same study area over approximately the same time period. A potential explanation for higher susceptibility of wolves to snaring is that they move further and over larger areas than cougars, increasing their encounter rates with bait stations (K. Knopff and N. Webb, University of Alberta, unpublished data). Further reductions in cougar susceptibility to wolf snares might be possible if differences in wolf and cougar habitat selection are exploited by trappers to diminish the probability that cougars will access areas where bait is placed and snares are set (Alexander et al. 2006, Kortello et al. 2007, Atwood et al. 2007). In addition, carrion bait can be used to attract wolves and maintain their presence in an area, but snares can be set near canid-specific lures several hundred meters away from bait carcasses to limit incidental capture of non-canid scavengers (G. Klassen, Alberta Trappers Association, personal communication). Trappers who check their bait stations frequently (e.g., daily instead of weekly) might be able to reduce the number of cougar captures by deactivating snares when they notice cougars accessing the bait.

MANAGEMENT IMPLICATIONS

My study highlights the potential importance of indiscriminate harvest techniques for non-target species captured incidentally in terrestrial systems. A strong propensity to scavenge makes cougars susceptible to carrion baiting techniques used to attract carnivores so that they can be trapped or snared. Managers working where snaring or trapping using carrion bait is permitted for species other than cougars, including snaring or trapping of coyote (*Canis latrans*), bobcat (*Lynx rufus*), and lynx (*Lynx canadensis*), might need to consider incidental mortalities when setting harvest quotas for cougars. Because incidental mortalities can vary among years, I recommend maintaining flexible hunting quotas that can be adjusted to compensate for the previous year’s mortality.

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CHAPTER 4

COUGAR KILL RATE AND PREY COMPOSITION IN A MULTI-PREY SYSTEM: INFLUENCE OF SEASON, DEMOGRAPHY, AND PREY VULNERABILITY

Developing effective management strategies for ungulates subject to large carnivore predation depends on reliable estimates of the components of predation such as kill rate and prey composition, but obtaining these data can be difficult. Logistical constraints associated with studying large carnivores tend to result in small sample sizes and limited monitoring duration. Moreover, many studies provide data from only one season (usually winter), which may not extrapolate well to annual predation rates (Sand et al. 2008). Recent applications of Global Positioning System (GPS) telemetry provide an efficient means to obtain large sample sizes over long monitoring periods in all seasons when investigating large carnivore predation (Anderson and Lindzey 2003, Webb et al. 2008, Chapter 2). I used a GPS telemetry approach to study cougars (*Puma concolor*) foraging in a seasonal multi-prey environment in west-central Alberta. I aimed to census cougar predation on ungulates during year-round monitoring to help address uncertainty surrounding 4 key aspects of cougar predation: 1) cougar kill rate, 2) the influence of season on cougar predation, 3) the influence of cougar population structure on predation, and 4) whether or not cougars target vulnerable prey. Clearing up uncertainty in each case will help ecologists and wildlife managers to better interpret and anticipate cougar impacts on ungulate prey.

Disagreement exists over the rate at which cougars kill ungulates, and estimates vary among studies by >350% within cougar age-sex classes (e.g., 15 vs. 53 ungulates/year for adult females; Table 4.1), representing substantial variation in the capacity for cougars to affect ungulate populations. Past estimates often were derived from potentially unreliable energetic models or models based on telemetry location clusters (see discussion in Laundré 2005), and even where direct field observations were employed, sample sizes tended to be small and/or monitoring durations short (Table 1). Approaches to calculating kill rate also vary among studies, and some methods bias parameter estimates, especially over short monitoring intervals (Hebblewhite et al. 2003). Thus, determining which estimates are best or how much of the variation among studies can be ascribed to ecological versus methodological differences is challenging. As Laundré (2005) points out, GPS telemetry studies where actual predation sequences are monitored in the field are needed to provide data capable of confronting disagreement among previous estimates and resolving uncertainty over the number of ungulates cougars actually kill. This chapter describes the first attempt to capture these data.

Although cougar researchers acknowledge the influence of season on predation patterns, moreover, they are divided about its effects. Some speculate that cougars will kill ungulates more frequently in winter because they switch to non-ungulate prey in summer (Hornocker 1970), because harsh environmental conditions (e.g., deep snow) cause ungulates to congregate and become more vulnerable in winter (Laundré 2008), or to account for the extra energetic costs of thermoregulation (Murphy 1998). Others expect higher kill rates in summer just after the ungulate birth pulse in May–June when vulnerable juveniles are plentiful (Nowak 1999, Laundré 2008). Available evidence regarding these hypotheses is contradictory. Whereas Cooley et al. (2008) reported no effect of season on kill rate, both Murphy (1998) and Nowak (1999) reported seasonal effects, but in opposite directions. I tested among competing hypotheses by evaluating seasonal variation in kill rates in terms of both frequency and biomass and relating these to prey composition.

Demographic structure of predator populations also can influence predation rates (Taylor 1984), and because human activities (e.g., hunting) often affect cougar demography (Robinson et al. 2008) understanding how population structure shapes cougar predation is important. Yet, although most studies indicate that kill rate varies by cougar age, sex, and reproductive class (Table 4.1), the reported magnitude and direction of this variation is inconsistent, and only Murphy (1998) and Anderson and Lindzey (2003) offer predation data for all age-sex classes from the same study site. Moreover, whether metabolic requirements drive variation in kill rate (Ackerman et al. 1986, Laundré 2005), or if other factors such as experience (Murphy 1998) also play a role remains unclear. To shed more light on these subjects, I estimated kill rate for different cougar demographic classes and explored potential drivers of variation among them. I also examined how prey composition varied by cougar class (e.g., Ross and Jalkotzy 1996), because this might drive variation in species or class-specific predation rates as cougar demography changes in multi-prey systems.

Finally, whether cougars are selective predators preferring vulnerable prey (as suggested by Pierce et al. 2000), or random predators that kill prey as available within normal prey size limits (as suggested by Husseman et al. 2003) has ecological consequences (e.g., Wilmers et al. 2007). To test between the different views, I evaluated cougar prey composition in response to seasonal shifts in prey vulnerability. The reproductive vulnerability hypothesis (Lima and Dill 1990) states that temporal variation in the reproductive physiology and behavior of animals will produce associated shifts in vulnerability to predation. If cougars select vulnerable prey they should target female ungulates during late gestation and early post-parturition when they are burdened by a heavy fetus or young neonate (Molinari-Jobin et al. 2004, Owen-Smith 2008), and males during the rut when they are physically weakened by fighting, more solitary, and less vigilant (Fitzgibbon 1990a, Owen-Smith 2008). Similarly, I expected cougars focusing on easier prey to exhibit disproportionate predation on juvenile ungulates in early summer when they are especially weak and vulnerable (Fitzgibbon 1990b, Testa et al. 2000).

Table 4.1: A review of published estimates of ungulate kill rate by cougars in North America

Source	**Location**	**Primary Prey[a]**	**Kill Rate[b]**								**Estimation Technique[c]**	**Calculation Technique[d]**	**Sample Size[e]**	**Monitoring Period[f]**
			UC	**UM**	**UF**	**AM**	**SM**	**AF**	**SF**	**FG**				
Connolly (1949)	UT	MD	0.73								Snowtracking	Ratio	≥26	<4
Hornocker (1970)	ID	MD, ELK	0.27-0.38								Model (E)	N/A	N/A	N/A
Hornocker (1970)	ID	MD, ELK								1.17	Snowtracking	Ratio	2	15
Shaw (1977)	AZ	MD						0.67		1.04	Model (LC-R)	N/A	4	N/A
Ackerman et al. (1986)	UT	MD				0.83		0.44		0.67-2.26	Model (E)	N/A	N/A	N/A
Ackerman et al. (1986)	UT	MD								1.57	Radiotelemetry	IKI	2	11
Harrison (1990)	BC	BS, MD								1.67	Radiotelemetry	IKI	2	34
Beier et al. (1995)	CA	MD	0.93								Radiotelemetry	Ratio	≤26	N/A
Murphy (1998)	WY	ELK, MD				0.94	0.64	0.64	0.69	0.98	Radiotelemetry	IKI	4	27
Nowak (1999)	OR	MD, ELK			0.92						Radiotelemetry	IKI	7	44
Janis & Clark (2002)	FL	WTD, FH		0.90	1.33						Model (LC-R)	IKI	8.5	136
Anderson & Lindzey (2003)	WY	MD, ELK				0.91	0.74	1.01	0.97	1.31	Model (LC-G)	Ratio	2.2	84

Laundré (2005)	ID	MD			0.37		0.29		0.85	Model (E)	N/A	N/A	N/A
Mattson et al. (2007)	AZ	ELK, MD			0.95	0.88	0.76	1.17		Model (LC-G)	IKI	2.5	N/A
Cooley et al. (2008)	WA	WTD, MD	0.74	0.91					1.20	Radiotelemetry	IKI	<5	<11
Laundré (2008)	ID	MD			0.47		0.49		0.59	Model (LC-R)	Ratio	12.6	3
Laundré (2008)	ID	MD					0.47		0.59	Model (LC-R)	Ratio	7	51
This study	AB	WTD, MD, MO			0.67	0.59	0.80	0.46	0.90-1.30[g]	GPS Telemetry	Ratio	10[h]	152

[a] Prey constituting >20% of cougar diet or primary prey available to cougars where diet was not reported: MD = mule deer, WTD = white-tailed deer, MO = moose, BS = bighorn sheep, FH = feral hog (*Sus scrofa*).

[b] Kill rate is ungulates/week: UC = cougar of unknown age-sex, UM = male cougar of unknown age, UF = female cougar of unknown age or reproductive status, AM = adult male, SM = subadult male, AF = adult female, SF = subadult female, FG = family group.

[c] Kill rate was either estimated directly by visiting kills in the field (snowtracking, radiotelemetry, or GPS telemetry), or indirectly using models (E = energetics model, LC-R = location cluster model based on radiotelemetry, LC-G = location cluster model based on GPS telemetry). In the case of Mattson et al. (2007) and Anderson and Lindzey (2003) field data were used to parameterize logistic regression location cluster models, but the models were used instead of field data to estimate kill rates.

[d] Calculation technique can be either ratio or inter-kill (see Hebblewhite et al. 2003).

[e] Sample size is the average number of cougars used per demographic category estimate.

[f] Monitoring period is the average number of days monitored per cougar used in each estimate.

[g] These represent separate estimates for FG with kittens <6months (lower estimate) and >6 months (higher estimate). Thus, in this study, I estimate kill rate for 6 cougar demographic classes, not 5.

[h] Kill rates were calculated more than once for the same cougar if it transitioned among demographic categories during my study.

STUDY AREA

I studied cougar predation in west-central Alberta, Canada during 1998-2008. I pooled data from 2 adjacent study areas representing one cougar population: the Bow Valley (BV) including portions of Banff National Park, and Clearwater County (CC) east of the Banff and Jasper National Park Boundaries (Figure 4.1). The study area was ecologically diverse, containing alpine, sub-alpine, montane, and boreal foothills ecoregions. Conifer forests dominated the landscape and were primarily composed of lodgepole pine (*Pinus contorta)*, white spruce (*Picea glauca*), Englemann spruce (*P. engelmannii*), and Douglas fir (*Pseudotsuga menziesii*), with occasional pockets of black spruce (*P. mariana*) and tamarack (*Larix laricina*) in low-lying areas, and subalpine fir (*Abies lasiocarpa*) at higher elevations. Aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) were patchily distributed, as were grasslands. Elevation varied between 849–3102m, and topographical complexity increased from flatlands in the east to rugged mountains in the west (Figure 4.1). Higher elevations consisted primarily of alpine meadow, rock, and ice. Industrial, residential, and agricultural developments were common, but varied in intensity throughout the study area, with higher development in the eastern portion of CC and along the Bow River Corridor in BV. The region's climate consisted of wet springs, dry summers, and cold, snowy winters. Westerly winds, known locally as Chinooks, provided periodic warming during winter, confining substantial snow accumulation to higher elevations and north aspects.

Potential ungulate prey for cougars included elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), feral horses (*Equus caballus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Woodland caribou (*Rangifer tarandus*) were present at extremely low density. Non-ungulate prey included beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), snowshoe hare (*Lepus americanus*), and grouse (family: Tetraonidae). Large domestic stock (e.g., cattle and llama) and pets (e.g., cats and dogs) were available as prey also, primarily on private lands in the eastern portion of CC. Other carnivores including bobcat (*Lynx rufus*), lynx (*L. canadensis*), coyote (*Canis latrans*), wolf (*C. lupus*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*), and grizzly bear (*U. arctos*) were present as potential prey and competitors for cougars.

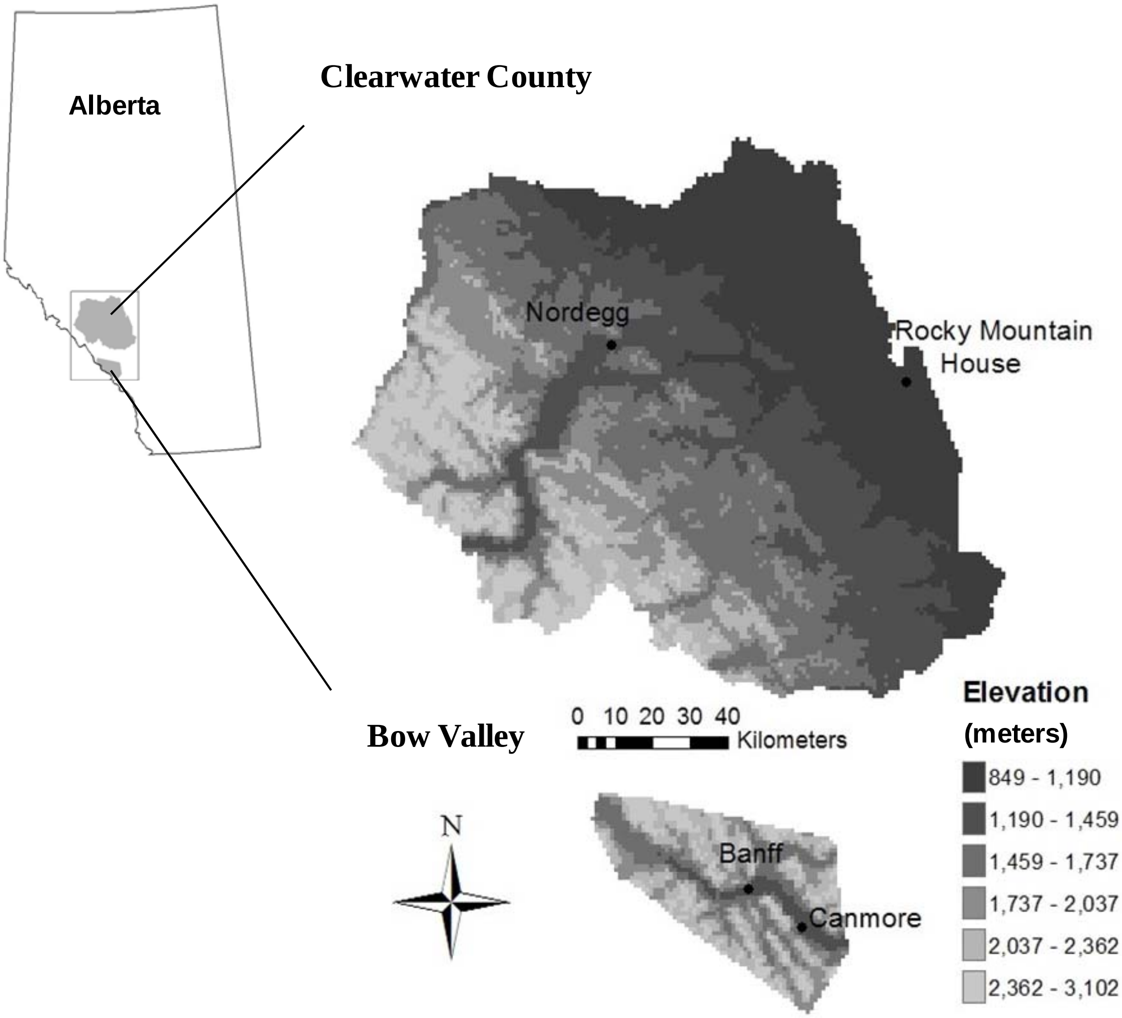

Figure 4.1: The location of the Clearwater County (CC) and Bow Valley (BV) study areas in west-central Alberta, Canada. Elevation and selected towns are displayed.

METHODS

Capture and Monitoring

Cougars were treed by hounds in winter and immobilized with chemical agents using a dart gun (Hornocker 1970). Procedures were approved by the University of Idaho Animal Care and Use Committee (No. 2002–20) in BV and the University of Alberta Animal Care Committee (No. 479505) in CC. In BV, 9 cougars were captured by A. Kortello between November 2000 and April 2003 using Ketamine (Vetalar®, Bioniche Animal Health Canada, Inc. Belleville, Ontario, Canada) and medetomidine (Zalopine®, Orion Corporation, Espoo, Finland) at an intended dose of 2.5 and 0.08 mg/kg respectively. In CC, I captured 44 cougars between December 2005 and May 2008 using 3 mg/kg zolazepam-tiletamine (Telazol®, Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and 2 mg/kg xylazine (Rompun®, Bayer, Inc., Toronto, Ontario, Canada).

Once immobilized, I weighed, measured, sexed, and aged cougars. I estimated age using a combination of tooth color and wear characteristics (Ashman et al. 1983, Shaw 1986), pelage spotting progression (Shaw 1986), and gum-line recession (Laundré et al. 2000). I classified cougars as kittens (still with mother), sub-adults (dispersal until 2.5–3 yr), or adults (>2.5–3 yr). I fitted cougars with one of three brands of Global Positioning System (GPS) radiocollar (Lotek 4400S—Lotek Engineering, Newmarket, Ontario, Canada, H.A.B.I.T VHF/GPS—H.A.B.I.T research, Victoria, British Columbia, Canada, or Televilt GPS-Simplex—Televilt International, Ramsberg, Sweden), or a Lotek LMRT-3 very high frequency (VHF) collar. Upon completion of handling, cougars were given 0.125 mg/kg yohimbine (Yobine®, Lloyd Laboratories, Shenandoah, Iowa, USA) to reverse xylazine, or 0.4 mg/kg atipamezole (Antisedan®, Pfizer Animal Health, Kirkland, Quebec, Canada) to reverse medetomidine and were released.

GPS collars were programmed to obtain a location at either 2 or 3 hour intervals (i.e., 8–12 fix attempts/day). I attempted to download data from each collar fortnightly, and I visited clusters of GPS locations as soon as possible thereafter to identify predation events. I considered a cluster any combination of ≥2 locations occurring within 200 m of each other and within a temporal window of 6 days (Chapter 2). In BV and prior to November 2007 in CC, I attempted to visit nearly all identified clusters. After 1

November 2007 in CC I employed a logistic regression model to screen clusters with a near-zero probability of predation from the set I visited in the field (Chapter 2). Cougars that were uncollared or VHF collared also were snowtracked opportunistically to locate predation events during 1998–2008.

Characteristics of Prey

I identified animal remains found at GPS location clusters as either predation or scavenging events provided there was evidence that the cougar had killed and/or fed on the carcass. I assigned predation if I found remains with evidence of being killed by a cougar, e.g., bite marks and hemorrhaging on the neck or a clear predation sequence played out by tracks in the snow at fresh kills. Where such information was not available, I assigned predation if the age of the remains closely matched the dates over which the cluster was created and there was no evidence to contradict cougar predation. I assigned scavenging in cases where the animal had been killed by something other than a cougar (e.g., remains at a trapper bait station, or from a wolf-killed, hunter-killed, or road-killed animal), or if the carcass age greatly preceded the dates the cougar spent at the cluster (Chapter 3).

I identified species of prey by anatomical, skeletal, and pelage characteristics (Stelfox 1993). I assigned prey to one of three age classes: young of the year (<1 yr), yearling (≥1 yr, ≤2 yr), or adult (>2 yr), as determined by size, degree of epiphyseal fusion, and tooth eruption and wear (Stelfox 1993). I used presence or absence of antlers or pedicles and other cranial characteristics (Stelfox 1993) to determine sex. If insufficient evidence existed to provide certain identification of species, age, or sex, I recorded “unknown”. I assigned each predation event either to winter (15 Oct – 14 Apr) or summer (15 Apr – 14 Oct) using the date of the first GPS location at a predation cluster (GPS collared cats), or the estimated mortality date (for kills located via snowtracking). I selected seasonal cutoffs to encompass broad shifts in temperature, daylight, and snow accumulation and to ensure the pulse in neonatal availability (i.e., May – Jun) was encapsulated within one season.

Because I usually visited kill sites after cougars had consumed their prey, I was unable to obtain biomass estimates in the field. Instead, I assigned approximate live weights to prey based on literature values (Table 2). For moose, elk, deer (white-tailed and mule deer combined), and bighorn sheep I assigned sex-specific weights to adults based on average values for Alberta ungulates (Renecker and Hudson 1993). Data on feral horse weights in west-central Alberta were unavailable, and I estimated average adult weight using known weight of similar-sized domestic horses. I obtained weights for yearling and young of the year ungulates were using a von Bertalanffy growth equation of the form $M(t) = A[1 - 1/3e^{-K(t - I)}]^3$ (Monteith et al. 2009), where $M(t)$ = mass (kg) at age t, A = maximum weight ($t = \infty$), K = growth rate, and I = the age at inflection point (days).

I did not differentiate between sexes for juveniles and yearlings and I used adult female weights for each species (Table 4.2) to define A, and I assigned values to K (0.0049) and I (140) so that the resulting curve roughly approximated a number of published ungulate growth curves (e.g., Anderson et al. 1974, Schwartz 2007, Hudson and Haigh 2002, Monteith et al. 2009). I then assigned median weights from the curves to each of 4 age brackets (0–3 months, 3–6 months, 6–12 months, and 12–24 months; Table 2). If I could not determin ungulate age class, I assigned yearling weight. If I knew age but could not distinguish sex, I used the mean adult weight [i.e., (AM+AF)/2]. Age-sex class was often difficult to determine for non-ungulate prey (generally little remained of the carcass) and I assigned a single average weight given by Soper (1964) for the species.

Table 4.2: Ungulate weights used to calculate kill rate (kg/day) and prey composition (percent biomass) for cougars in west central Alberta, Canada.

	Species				
Age/Sex Class	**Deer**	**Elk**	**Moose**	**Bighorn Sheep**	**Feral Horse**
Adult Male	95[a]	320[a]	450[a]	117[a]	420[b]
Adult Female	70[a]	230[a]	418[a]	65[a]	420[b]
Yearling (12-24 months)	55[c]	181[c]	330[c]	51[c]	331[c]
YOY (6-12 months)	38[c]	124[c]	226[c]	35[c]	227[c]
YOY (3-6 months)	21[c]	68[c]	123[c]	19[c]	124[c]
YOY (0-3 months)	10[c]	33[c]	60[c]	9[c]	61[c]
Unknown	54[c]	178[c]	323[c]	50[c]	325[c]

[a] Estimates obtained from Renecker and Hudson (1993)

[b] Estimated using known weight of similar sized domestic horses

[c] Median weights for each non-adult age class were derived from a von Bertalanffy growth equation of the form $M(t) = A[1 - 1/3e^{-K(t-I)}]^3$, where $M(t)$ = mass (kg) at age t, A = maximum weight (I used weight of AF), K = growth rate (we used 0.0049), and I = the age at inflection point (I used 140 days).

Prey Composition

I calculated the species and age-sex composition of prey in cougar diets using all predation events where these prey characteristics were known. I calculated species composition both as percent frequency and percent biomass. I collapsed prey into 3 categories: small ungulates (e.g., deer, sheep, goats), large ungulates (e.g., elk, moose, feral horses), and non-ungulate prey, and used chi-square tests to compare prey composition between adult male, adult female, and sub-adult cougars and between seasons within demographic classes. These and all other statistical analyses reported in this chapter were performed in STATA SE 9.0 (StataCorp, College Station, Texas, USA).

I also analyzed monthly variation in ungulate prey composition (I pooled data from all cougars) to test hypotheses about prey vulnerability. If cougars selected vulnerable prey, I expected greater representation by males in fall, females in spring, and overrepresentation of juveniles immediately following the birth pulse. Assuming 80% of all ungulates in west-central Alberta were female with an annual fecundity rate of 1.5 gives a post-birth proportion of 54.5% juveniles in the ungulate population, which probably overestimated the true reproductive capacity of the ungulate guild occurring in west-central Alberta (Demarais and Krausman 2000). I therefore considered selection for juveniles to occur in months where they comprised >55% of predation events.

Kill Rate

To ensure consistency and avoid potential bias, I used only data from cougars monitored using GPS telemetry where collar fix success was >45% to calculate kill rate (Chapter 2). Although I point out in chapter 2 that monitoring periods must be long (preferably >100 days over a 180 day period) to reduce the influence of sampling error on kill rate estimation, restricting calculations to shorter monitoring periods that reflect changes in season and demography might be appropriate if these factors influence kill rate. I did not control for these covariates in my preliminary analyses in chapter 2 and this may partially account for the high variation in kill rate in sub-samples. I therefore chose to calculate kill rates for all cougars continuously monitored for ≥ 4 weeks (28 days) in a given season and demographic class. I used the ratio estimator (Hebblewhite et al. 2003), which is both more conservative and more accurate than the inter-kill method (e.g., Murphy 1998, Cooley et al. 2008) which truncates the denominator in the rate estimator to the period between the first and last kills in a predation sequence and eliminates monitoring periods where ≤ 1 kill was made. I used total monitoring time as the denominator for rate estimation and both number of kills and kilograms of prey as numerators, yielding frequency (events/week) and biomass (kg/day) metrics. I calculated frequency metrics only for ungulates, as non-ungulate prey <8 kg are likely to be underestimated in my sample (Chapter 2). I based biomass estimates on the live weight of all prey and therefore will overestimate cougar consumption. I did not attempt to correct for this overestimation because I did not measure loss to scavengers, decomposition, or carcass abandonment, and I was uncertain about the percent of prey biomass available for cougar consumption (e.g., probably >90% for neonates, an unknown quantity less for adult deer, and much less for adult moose or feral horses where cougars cannot access bones and marrow). Consequently, any correction factor I applied would be arbitrary.

To provide results comparable to other studies, I first calculated the average annual kill rate for cougars using individuals as the unit of analysis and pooling data across seasons and demographic classes. I then estimated season-specific kill rates for six different cougar age-sex and reproductive classes: sub-adult female, sub-adult male, adult male, adult female, adult female with kittens <6 months, and adult female with kittens >6 months. Kill rates were calculated more than once for an individual cougar in a given season if the animal transitioned between age and/or reproductive categories during the study. I visited den sites to obtain initial kitten counts and then used track counts in snow, dirt or mud, and occasional visual observations to monitor kitten retention. I aged kittens traveling with females at capture using spotting progression, body size, and track size, and counted them when treed or by snowtracking.

I assessed the effect of season on kill rate while controlling for demographic variation using a 2-tailed paired t-test for individuals monitored ≥ 28 days in the same demographic class in both summer and winter. Next, I assessed the influence of demography on kill rate using a single factor analysis of variance (ANOVA) in each season. Demographic and season-specific monitoring periods for each cougar were the units of analysis. Post-hoc comparisons using Tukey's test determined which demographic classes differed (Day and Quinn 1989). I estimated annual kill rates for each demographic class using the mean of season-specific values.

To test the hypothesis that kill rate increases as a consequence of the ungulate birth pulse in spring (e.g., Nowak 1999, Sand et al. 2008), I calculated the average interval between the first location fixes at consecutive predation events by month (intervals were assigned to the month in which they ended) for each cougar to determine whether the inter-kill interval (IKI) declined during and immediately after the birth pulse. I then evaluated the relationship between IKI and proportion of juvenile ungulates in monthly cougar diets using a Pearson's correlation. I used IKI for these analyses to avoid problems with calculating rates over extremely short monitoring periods (e.g., a few days) during months where monitoring was truncated due to capture or collar failure.

To provide a more mechanistic understanding of variation in cougar kill rates, I divided cougar IKI into search time (a function of the probability of encountering prey and the probability killing prey given an encounter) and handling time (time spent consuming prey). I defined handling time as the number of GPS locations obtained at a predation cluster divided by the collar fix success over the duration of the cluster, and multiplied by the collar fix rate (e.g., 3 hours). I calculated search time by subtracting the handling time of the prey killed at the beginning of an IKI from the total length of the interval. Negative search times could be calculated if a second prey was killed (ending the initial IKI) while the first prey was still being handled (simultaneous handling of multiple prey). In such cases, I designated search times as zero.

I tested the difference between average search and handling time during summer and winter using t-tests where each predation event was the unit of analysis. I also controlled for prey size (i.e., handling time/kg of prey) in a similar analysis to test the hypothesis that per kilogram handling times will be reduced in summer, possibly as a consequence of increased contest competition with bears (e.g., Murphy et al. 1998) or more rapid decomposition of carcasses during warmer months. I then obtained monthly averages of search and handling time and correlated these with the proportion of juveniles in the diet to determine how each component of predation varied as a function of prey composition.

I regressed cougar body mass against kill rate (kg prey/day) in each season to test the hypothesis that kill rate is driven by metabolic requirements (Ackerman et al. 1986, Laundré 2005). I estimated weights for family groups by adding 15 kg per kitten <6 months old and 34 kg per kitten >6 months old to the capture weight of the mother. When comparing my regressions to those estimated in other studies (i.e., Laundré 2005) I first converted all kill rate estimates into kilograms of live weight/day. I also tested Murphy's (1998) hypothesis that cougar kill rate is related to experience, and not necessarily metabolic needs alone. If this were true, adults should have higher kill rates (kg prey/kg cougar) than sub-adults. I excluded family groups because of different metabolic needs associated with kitten growth (Ackerman et al. 1986) and compared adult and sub-adult data for each season separately using 1-tailed t-tests.

RESULTS

My sample of captured cougars included 30 adult females, 7 adult males, 6 sub-adult females, and 10 sub-adult males. Of these, 4 sub-adult females and 2 sub-adult males transitioned to adults and 9 adult females transitioned among reproductive classes while they were radiocollared. I monitored predation of 42 GPS collared cougars continuously over 9,543 cougar-days (mean = 227 days/cougar, SD = 127), split approximately evenly between summer (4,852 days) and winter (4,691 days) during 2002-2008. With the help of top-notch field crews, I visited >3,700 GPS location clusters and snowtracked cougars for >1,100 km, locating a total of 1,509 predation events. I visited predation sites an average of 25 days (SD = 26) after kills were made and all edible biomass had generally been consumed by the time I arrived. Because smaller prey often were consumed completely, age and sex were infrequently determined for non-ungulates and sex was almost never available from juvenile ungulates. However, I was able to identify species (white-tailed and mule deer combined as "deer") at 1,505 kills, age at 1,241 kills, and sex at 495 kills.

Cougars in west-central Alberta conformed to the killing and feeding behavior described elsewhere (e.g., Beier et al. 1995). I located a number of fresh kills (within 48 hrs of the predation event) while snowtracking or at GPS clusters (n = 73) and cougars generally killed prey by biting the neck, causing death by either compressing the trachea or breaking the spine. They occasionally crushed the skulls of smaller prey. After making a kill cougars dragged the carcass an average of 34 m to a cache location (SD = 52, n = 125). Cougars occasionally dragged carcasses long distances (e.g., >200 m) when prey were killed in open habitats without suitable cover for caching. Cougars tended to cache prey such that carcass visibility was reduced (e.g., under the low-hanging branches of conifer trees), and nearly always buried prey between feeding bouts under whatever debris was available (Figure 4.2). Presumably, this was an attempt by cougars to deter scavengers or slow decomposition. Despite extensive caching behavior by cougars, I noted avian and/or mammalian scavenging at 38% of predation sites I visited. Cougars sometimes capitalized on this activity, killing and consuming coyotes, foxes, lynx, and ravens at ungulate predation sites.

Prey Composition

Cougars killed a variety of wild prey including ungulates (white-tailed deer, mule deer, moose, elk, bighorn sheep, mountain goat, feral horse), carnivores (cougar, wolf, coyote, red fox [*Vulpes vulpes*], lynx, black bear, marten [*Martes americana*]), small mammals (beaver, porcupine, snowshoe hare, red squirrel [*Tamiasciurus hudsonicus*], hoary marmot [*Marmota caligata*]), and birds (grouse, ducks [*Anas* spp.], Canada geese [*Branta canadensis*], raven [*Corvus corax*]). The size of wild prey killed by cougars spanned 2 orders of magnitude ranging from red squirrels (0.35 kg) to adult moose and feral horses (>400 kg). Domestic animals (e.g., llamas, cattle, dogs) comprised <1% of predation events.

Figure 4.2: A male white-tailed deer killed and subsequently cached under debris by a collared cougar in west-central Alberta in 2007. Note the hind hoof in the upper right and the antlers in the lower left.

Wild ungulates made up most prey I identified in both relative frequency (84%) and biomass (96%). Deer were the most prevalent ungulate (frequency = 64%, biomass = 51%), and of the cases where I could distinguish deer species (n = 541) white-tailed deer dominated (68%). Most ungulate prey were either young of the year (43%) or adults (45%) with yearlings making up the remainder. Cougars tended to kill younger animals especially when preying on feral horses and moose (the largest prey available in west-central Alberta) and nearly all predation on these species (86%) involved animals <2 years old. Female prey made up 58% of all predation events where I identified sex.

Cougars exhibited seasonal shifts in prey composition (AM, $\chi_2^2 = 15.63$, $P < 0.001$; AF, $\chi_2^2 = 7.67$, $P = 0.022$; SA, $\chi_2^2 = 17.29$, $P < 0.001$). Cougars killed more large ungulates (e.g., moose, elk, feral horses) in summer, and in opposition to Hornocker's (1970) hypothesis, sub-adults shifted their diet to include substantially more non-ungulate prey (especially porcupines) in winter (Table 4.3). The age structure of cougar prey varied by season and the proportion of juvenile ungulates found at predation events increased ($\chi_2^2 = 43.70$, $P < 0.001$) during summer. Juvenile ungulates exceeded 55% of all prey killed by cougars (indicating selection) in July and August (Figure 4.3). In these months, juvenile ungulates also account for up to 46% of the biomass killed by cougars, despite their small size. Although not significantly different between seasons ($\chi_1^2 = 1.771$, $P = 0.183$), the proportion of male and female ungulate prey in cougar diet varied substantially by month over the course of the year (Figure 4.4). Female ungulates were killed most often in April – June, whereas the proportion of males peaked during August – November.

Species composition of prey also varied among cougar age-sex classes ($\chi_4^2 = 295$, $P < 0.001$; Figure 4.5). Large ungulates made up 48.4% of ungulates killed annually by adult males, but only 8.6% and 10.7% of the prey killed by adult females and sub-adults, respectively. Non-ungulate prey appeared more frequently in sub-adult diets (34.4%) than in those of either adult males (12.7%) or adult females (12.8%). Adult females focused predation on small ungulates (78.6%). When I considered biomass, the importance of large ungulates intensified for all age sex classes (AM = 78.0%, AF = 20.9%, SA = 25.2%), whereas the importance of non-ungulates subsided (AM = 2.0%, AF = 3.4%, SA = 12.2%). Niether the age ($\chi_4^2 = 1.41$, $P = 0.843$) nor sex ($\chi_2^2 = 0.74$, $P = 0.691$) of ungulate prey varied among sex and age classes of cougars.

Table 4.3: Seasonal comparison of the proportional frequency of prey in the diet of adult female, adult male, and sub-adult cougars. Results are presented for individual prey types and condensed prey categories using data from 1,428 predation incidents for 53 cougars in west-central Alberta, Canada during 2001-2008.

		Adult female		**Adult Male**		**Sub-adult**	
	Prey Type	**Summer** (n = 557)	**Winter** (n = 406)	**Summer** (n = 107)	**Winter** (n = 114)	**Summer** (n=153)	**Winter** (n = 91)
Individual Prey Types	Beaver	4.67%	1.72%	9.35%	5.26%	15.03%	4.40%
	BH Sheep	0.54%	5.42%	1.87%	6.14%	2.61%	12.09%
	Coyote	2.50%	3.20%	0.00%	0.88%	1.96%	4.40%
	Domestic	0.36%	0.99%	0.00%	0.00%	0.65%	3.30%
	Elk	4.49%	5.17%	12.15%	14.04%	2.61%	2.20%
	Deer	75.40%	76.85%	25.23%	43.86%	55.56%	37.36%
	Feral Horse	0.54%	0.00%	13.08%	10.53%	0.00%	0.00%
	Moose	5.75%	0.49%	36.45%	11.40%	13.07%	0.00%
	Porcupine	1.08%	0.74%	0.00%	0.00%	5.88%	26.37%
	Other	4.67%	5.42%	1.87%	7.89%	2.61%	9.89%
Condensed Categories	Non-ungulate	13.29%	12.07%	11.21%	14.04%	26.14%	48.35%
	Small ungulate	75.94%	82.27%	27.10%	50.00%	58.17%	49.45%
	Large ungulate	10.77%	5.67%	61.68%	35.96%	15.69%	2.20%

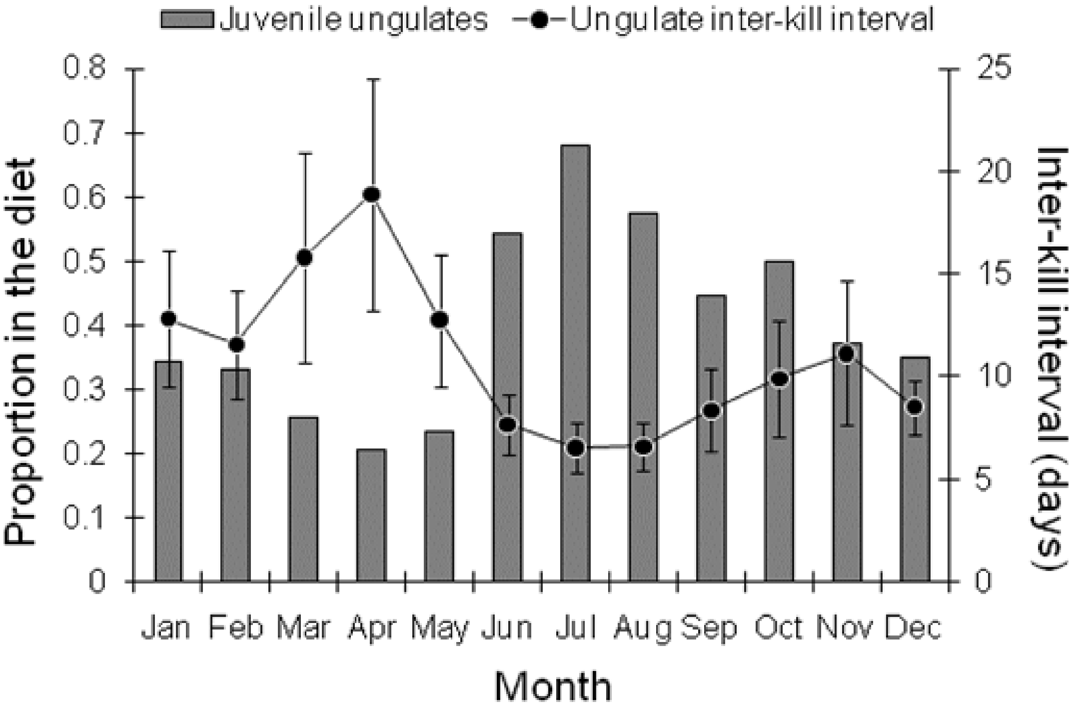

Figure 4.3: Monthly proportion of juvenile prey in cougar diet and the average ungulate inter-kill interval (bound by 95% CI) preceding kills made in each month in west central Alberta, Canada during 2001–2008. Proportions are derived from 1,229 kills where age of prey and date of death were known. Inter-kill intervals were estimated for 42 cougars from 1,090 kills where the date of the preceding ungulate kill was known. Individual cougars were the unit of analysis in each month, and data from all cougar age-sex classes were pooled.

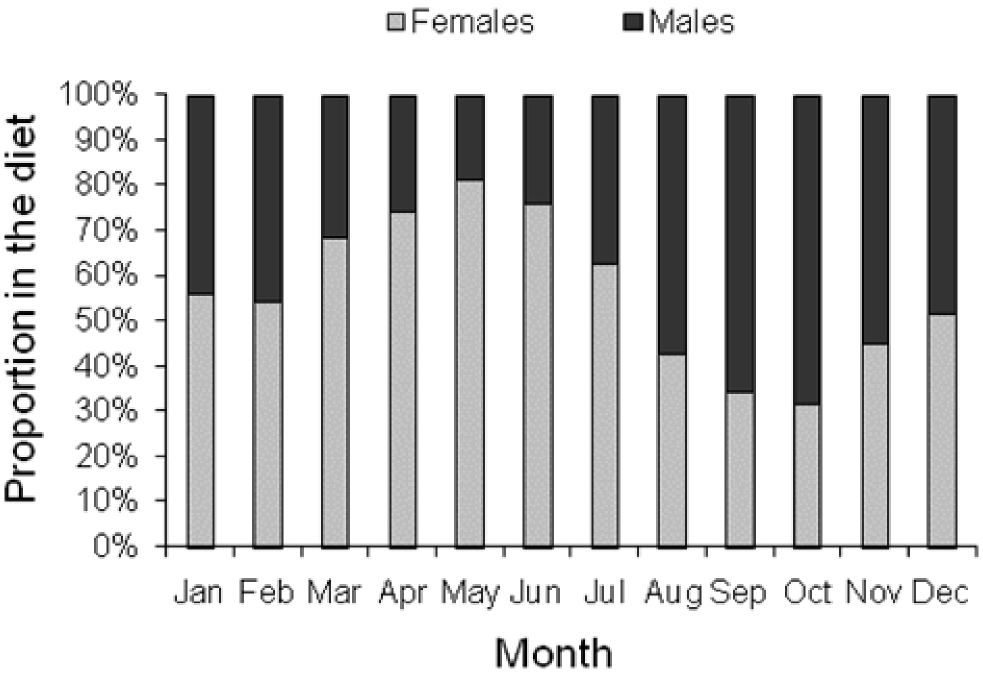

Figure 4.4: Monthly proportion of male and female ungulate prey in the diet of cougars in west-central Alberta, Canada during 1998–2008. Estimates are derived from 489 predation events where sex could be unambiguously identified (i.e., skull or reproductive organs present) and month of death was known. Because I was rarely able to identify the sex of juvenile prey, >80% of the data presented here were obtained from adult and yearling prey.

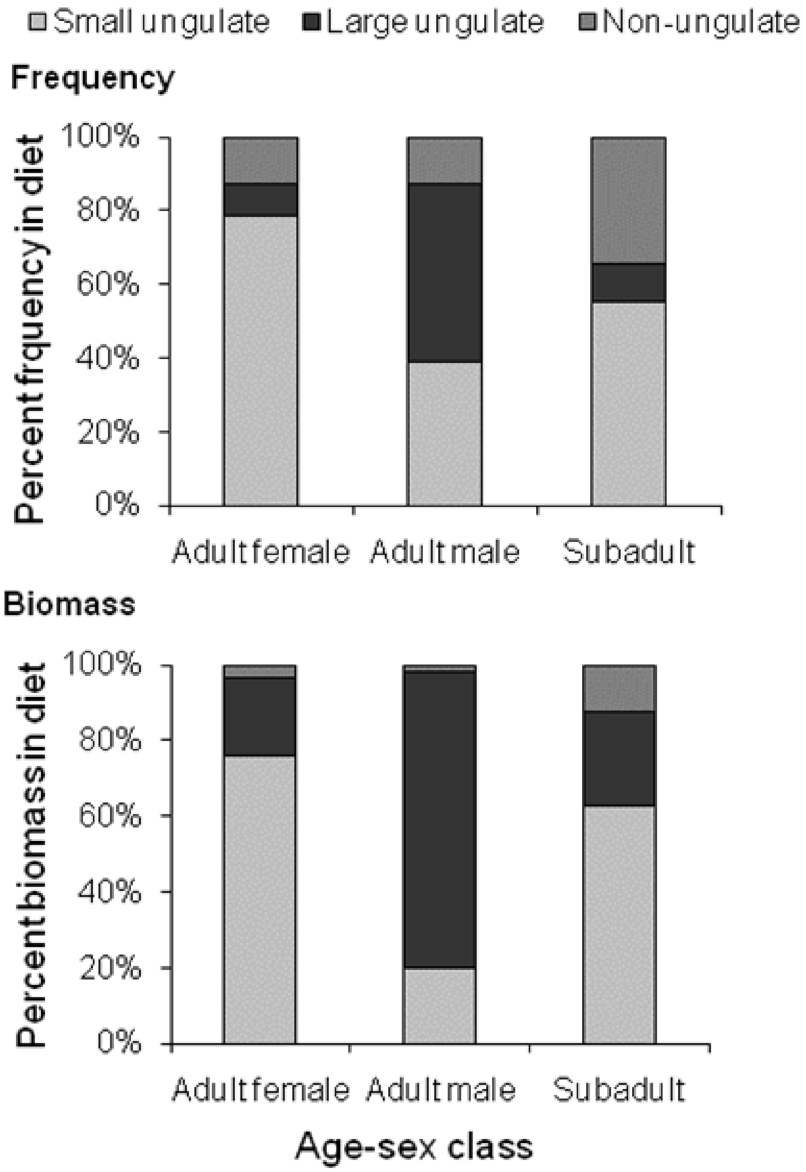

Figure 4.5: Composition of adult female, adult male, and sub-adult cougar diet expressed as frequency and biomass of non-ungulates, large ungulates (elk, moose, horse), and small ungulates (bighorn sheep, deer, mountain goat) in west-central Alberta, Canada during 2001-2008. Estimates were derived from 963 kills made by adult females, 221 kills made by adult males, and 244 kills made by sub-adults.

Kill Rate

I estimated kill rate using a subset of 1,326 kills located at telemetry clusters during continuous monitoring of GPS collared cougars. I did not calculate kill rates for cougars wearing H.A.B.I.T GPS collars because fix success averaged <35%. I calculated 85 season and demographic specific kill rates for which monitoring periods averaged 107 days (SD = 48.5). I did not calculate kill rate for 10 monitoring periods because their duration was <28 days. Cougar kill rate (not accounting for the influence of season or demography) averaged 0.8 ungulates/week (95% CI = 0.7–0.9) or 8.28 kg/day (95% CI = 7.13-9.41), but kill rates were variable among individuals (range = 0.24 – 1.38 ungulates/week and 2.88 – 18.60 kg/day). Moreover, ungulate IKIs varied within individuals during monitoring periods (Figure 4.6). Cougars occasionally made kills in rapid succession, but I also documented 52 intervals between ungulate kills that exceeded three weeks (21 days), the longest of which lasted 75 days. Cougars survived these periods by consuming other carnivores, small mammals, birds, and/or carrion.

I monitored 27 individual cougars that maintained demographic status across seasons. Using these paired data I found that, on average, cougars in west-central Alberta killed 1.49 times as many ungulates/week in summer ($\bar{x}$ = 0.951 ungulates/week, 95% CI = 0.797–1.105) as in winter ($\bar{x}$ = 0.639 ungulates/week, 95% CI = 0.497–0.782; t_{26} = -5.358, $P < 0.001$). Biomass killed also was slightly higher in summer ($\bar{x}$ = 8.60 kg/day, 95% CI = 6.68–10.52) than in winter ($\bar{x}$ = 7.79 kg/day, 95% CI = 5.64–9.94), but not significantly so (t_{26} = -0.931, $P = 0.360$). Increased frequency of ungulate killing in summer occurred in tandem with an increasing reliance on juvenile prey. Ungulate IKI varied substantially by month, reaching a high in April and dropping rapidly through the ungulate birth pulse (May – Jun) before increasing again after a low in July (Figure 4.3). Monthly variation in IKI was strongly and negatively correlated ($R^2 = 0.74$, $P < 0.001$) with the proportion of juvenile ungulates in cougar diet (Figure 4.3).

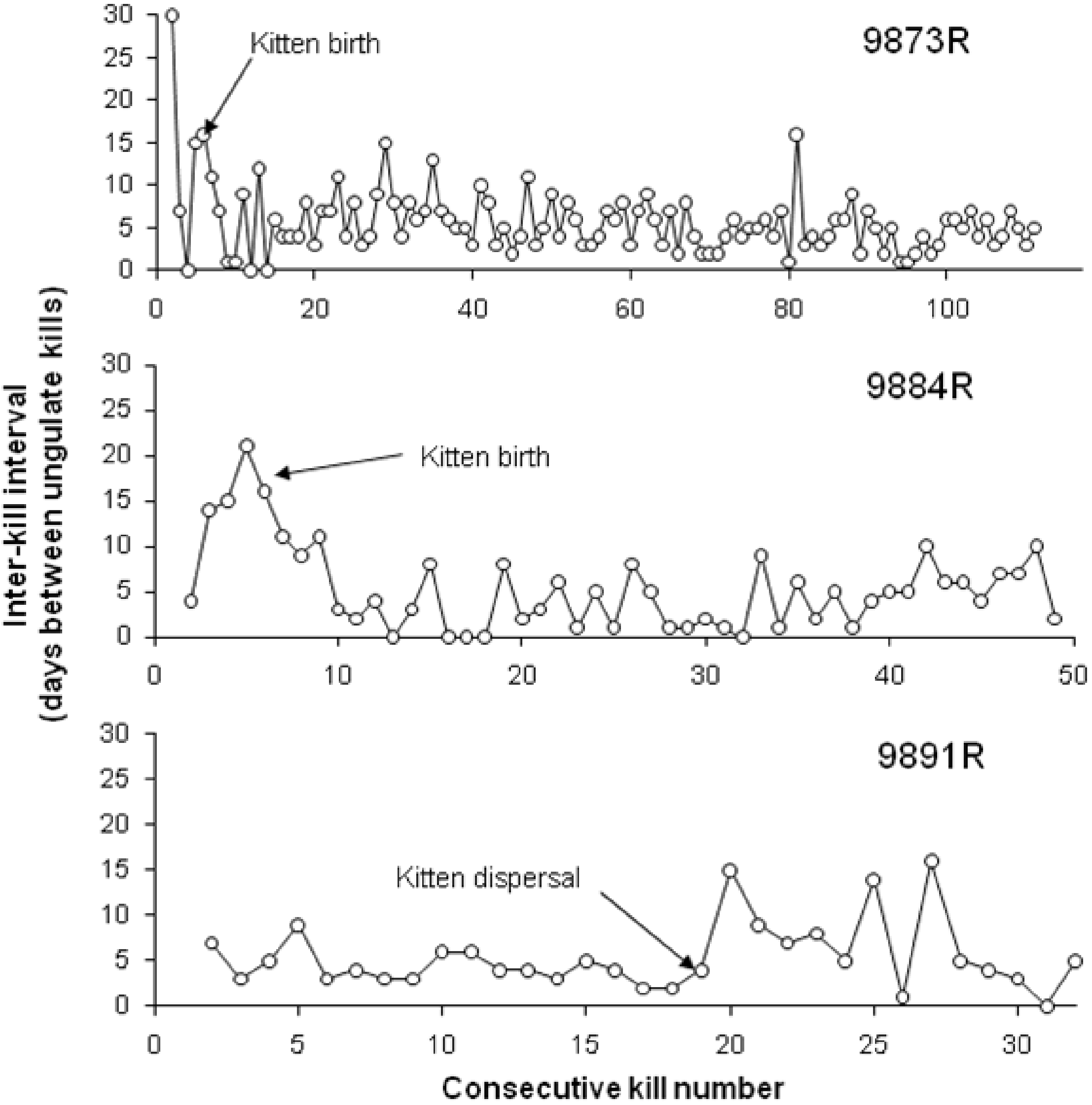

Figure 4.6: Examples of ungulate inter-kill interval timelines for three female cougars in west-central Alberta, Canada between 2005 and 2008. Note the high degree of variability in the amount of time between ungulate kills for all cougars, and the tendency for inter-kill interval to decline as kittens age after birth and increase again after kitten dispersal.

Average handling time of prey was 39% higher in winter ($\bar{x}$ = 78 hr, SD = 63.8) than in summer ($\bar{x}$ = 56 hr, SD= 46.8; $t_{1,239}$= -6.703, $P < 0.001$), and handling time was positively correlated with prey size ($R^2 = 0.21$, $P < 0.001$, n = 1,240). Thus, reduced inter-kill intervals in months where juveniles made up an increasing proportion of cougar diet were due in part to smaller prey. However, after controlling for prey size, I found that handling times were still 22% longer in winter ($\bar{x}$ = 2.20 hr/kg, SD = 3.9) than summer ($\bar{x}$ = 1.81 hr/kg, SD = 2.3; $t_{1,239} = -2.22$, $P = 0.013$), suggesting that other factors (e.g., scavenging by bears, more rapid carcass spoilage) might have contributed to the overall reduction in summer handling time.

Average duration of searching before making a kill also was lower in summer (summer = 117 hr, SD = 144; winter = 159 hr, SD = 207; $t_{1,036} = -3.78$, $P < 0.001$), contributing substantially to the overall reduction in inter-kill interval. Indeed, search time declined more than twice as fast as handling time for each incremental increase in the proportion of juvenile prey in cougar diet (Figure 4.7). Thus, increased encounter rates via greater prey abundance, greater vulnerability of prey to attack once encountered, and/or seasonal changes in searching intensity contributed more to higher cougar kill rate in summer than did reduced handling time.

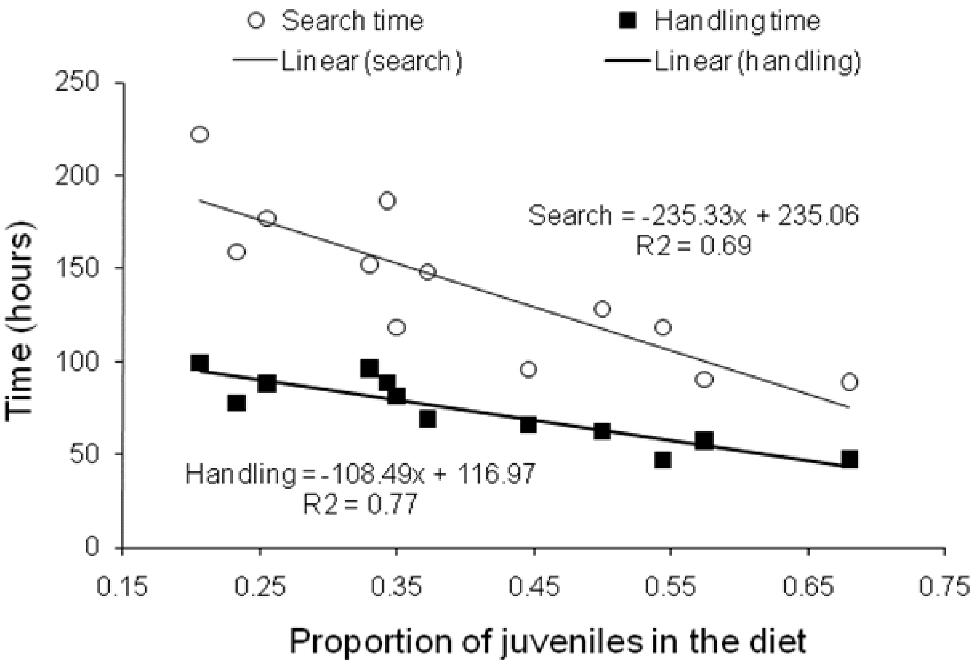

Figure 4.7: Relationship between the monthly proportion of ungulate juveniles in cougar diet and the average search and handling times during inter-kill intervals (n=1,211) by month in west-central Alberta, Canada during 2001-2008. The best fit linear regression equations and R^2 values are displayed.

Frequency of ungulate killing varied among cougar age-sex classes in both summer ($F_{5,30} = 6.85$, $P < 0.001$) and winter ($F_{5,43} = 13.3$, $P < 0.001$). Reproductive status had an especially profound impact: females with kittens >6 months old killed most frequently, followed by adult females with kittens <6 months old, adult females without kittens, adult males, sub-adult males, and finally sub-adult females (Figure 4.8). Results of Tukey's pairwise post-hoc comparison revealed that statistical differences were driven primarily by adult females with kittens >6 months, which killed significantly more frequently than adult males and sub-adults of both sexes in winter and all demographic classes except adult females with kittens <6 months in summer. The average number of ungulates killed per year was 24 for sub-adult females, 31 for sub-adult males, 35 for adult males, 42 for adult females, 47 for females with kittens <6 months, and 67 for females with kittens >6 months.

Biomass of prey killed by cougars also varied by demographic class in both seasons (summer: $F_{5,30} = 6.93$, $P < 0.001$; winter: $F_{5,43} = 9.27$, $P < 0.001$). Differences were primarily a result of the high biomass killed by adult males and females with kittens >6 months (Figure 4.8). Adult males killed greater mass of prey than all other demographic classes except adult females with kittens >6 months in winter, and significantly more than sub-adult females in summer. Adult females with kittens >6 months also killed significantly higher biomass than sub-adult females in summer, and significantly higher than both sexes of sub-adult in winter.

High biomass killed by adult females with kittens >6 months is consistent with the frequency of killing exhibited by this class of cougars (Figure 4.8). For adult males, on the other hand, frequency of killing is low relative to other age-sex classes, and high biomass is instead related to the larger species of ungulate prey (e.g., moose, feral horses) more often incorporated into their diet. The wide confidence interval surrounding the summer biomass estimate for sub-adult males (Figure 4.8) occurred because one approximately 2.5-year-old male (still without a stable home range) transitioned to killing moose like an adult male. The annual live-weight biomass of prey killed by cougars averaged 1,441 kg for sub-adult females, 2,051 kg for sub-adult males, 4,708 kg for adult males, 2,423 kg for adult females, 2,794 kg for females with kittens <6 months, and 4,280 kg for females with kittens >6 months.

Nearly all of my kill rate estimates were above the values predicted by Laundré's (2005) energetics model for cougars (Figure 4.9). Nevertheless, cougar body mass remained a significant predictor of the kilograms/day killed by cougars in both summer ($R^2 = 0.30$ and $P < 0.001$) and winter ($R^2 = 0.21$ and $P = 0.002$), lending support to the hypothesis implicit in energetics models that metabolic requirements are an important determinant of kill rate. However, *R*-squared values indicate that the majority of the variation in kill rate remained unexplained by a model based on energetics alone. Experience, for instance, appeared to play a role and I found that after controlling for body mass, adults killed nearly twice as much as sub-adults in both summer (adult = 0.183 kg of prey/kg of cougar/day sub-adult = 0.098 kg of prey/kg of cougar/day, $t_{25} = 4.078$, $P < 0.001$) and winter (adult = 0.148 kg of prey/kg of cougar/day, sub-adult = 0.080 kg of prey/kg of cougar/day, $t_{27} = 2.628$, $P = 0.007$).

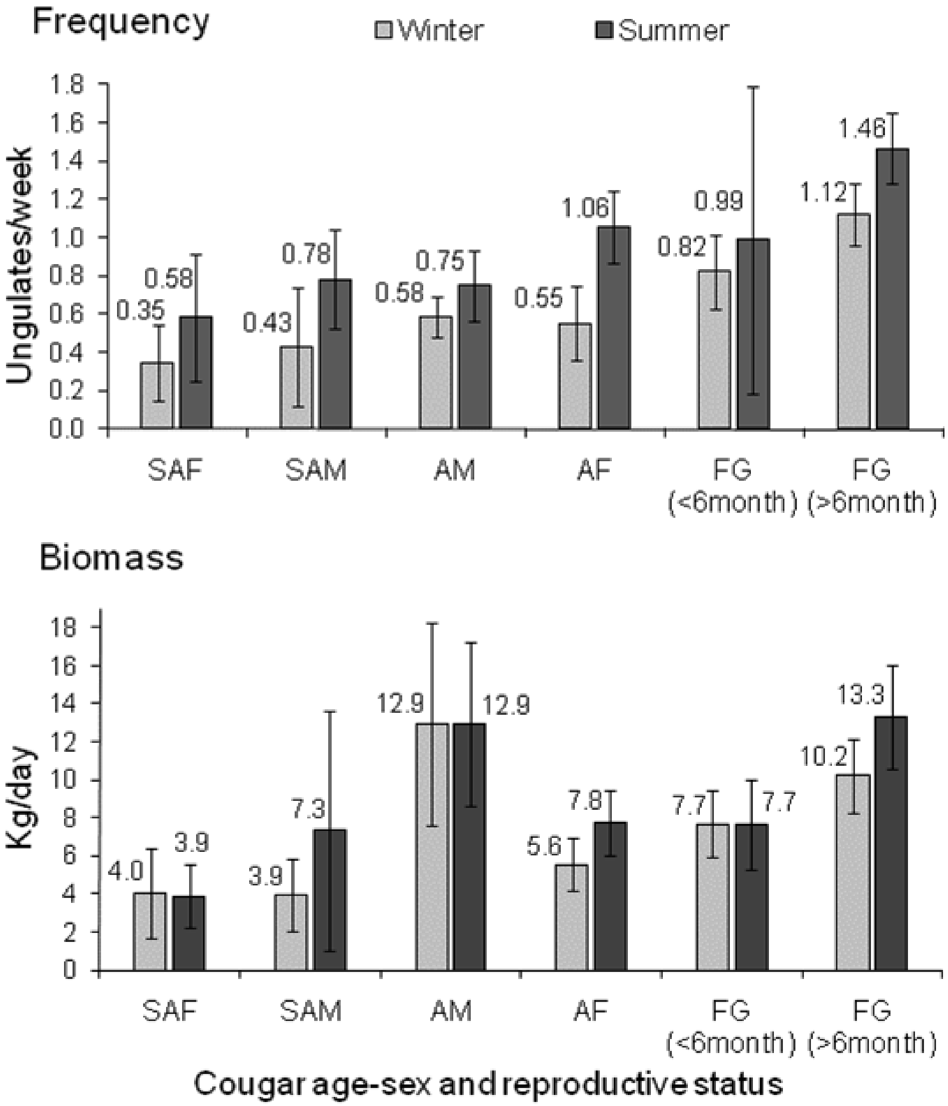

Figure 4.8: Cougar kill rates and associated 95% confidence intervals expressed as the frequency and biomass of prey for each demographic category and season in west-central Alberta, Canada during 2001-2008.

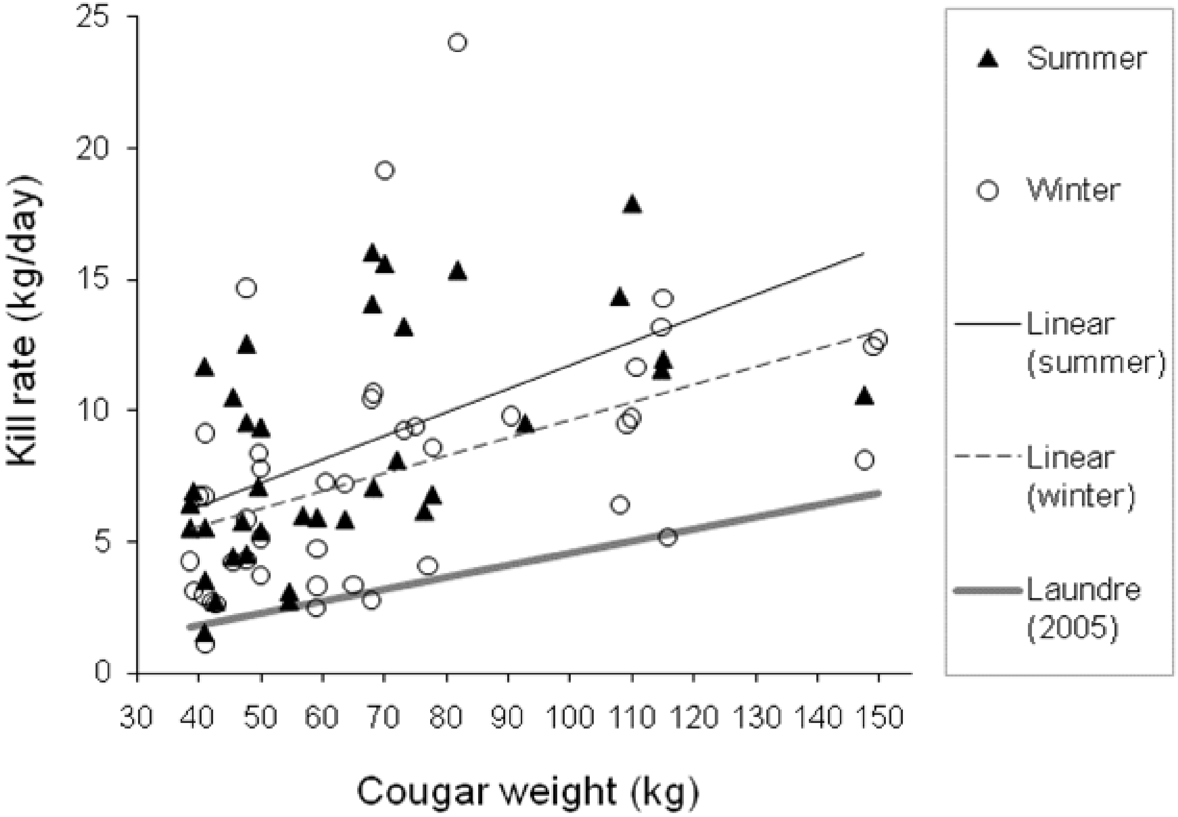

Figure 4.9: Relationship between cougar body mass (incorporating kitten weight for family groups) and kill rate (estimated live-weight kg of prey per day) in summer and winter in west-central Alberta, Canada during 2001–2008. Also displayed is the relationship between cougar mass and kill rate predicted by Laundré's (2005) energetics model. To facilitate comparison with my data, I used Laundré's (2005) average daily requirement of 0.0363 kg of prey/kg of cougar/day divided by the constant 0.79 he used to convert edible biomass to live-weight biomass (=0.0459 live-weight kg of prey/kg of cougar/day).

DISCUSSION

Kill Rate

Most of my annual kill rate estimates fell within the range of values reported for cougars elsewhere (Table 1), which is not surprising given the large variation among previous estimates. Adult females and family groups in west-central Alberta tended to kill closer to the high end of earlier estimates, whereas adult males killed at the lower end (in terms of frequency, not biomass). The ratio method I used to calculate kill rate is substantially more conservative (i.e., >25%; Hebblewhite et al. 2003) than the IKI estimator used in most other field studies of cougar kill rate. Thus, the adult cougar kill rates I found are among the highest recorded using field data. Sub-adults were less effective predators, and my kill rate estimates were lower than those given previously (Table 1). Two of the three previous estimates, however, used cluster models without field visitation (e.g., Anderson and Lindzey 2003, Mattson 2007), which tend to overestimate sub-adult kill rate (Anderson and Lindzey 2003; K. Knopff, University of Alberta, unpublished data).

My kill rate estimates indicate that adult cougars are highly effective predators, killing at rates at the upper end of those recorded for wolves in both frequency and biomass (Peterson and Ciucci 2003, Sand et al. 2008, Webb 2009). My estimates are especially inconsistent with lower values that have been proposed based on energetics calculations (Laundré 2005), and movement models (Laundré 2008) for cougars during summer in Idaho. The Idaho estimates differed from my summer estimates by as much as 365% in terms of frequency of killing and 538% in terms of live-weight biomass of prey. Because kill rate fundamentally influences the effect predators have on their prey, the discrepancy between studies represents a substantial difference in the capacity for cougars to impact ungulates. For instance, Laundré et al. (2006) used a deterministic population model and kill rates derived from energetics calculations (Laundré 2005) to analyze cougar-mule deer dynamics in southern Idaho, concluding that cougars did not contribute to the decline, or impede the recovery of mule deer between 1992 and 2004. Incorporating the higher kill rate values identified in my study would alter this conclusion considerably.

Some of the discrepancies in the kill rates listed in Table 1 are likely a result of inaccuracies associated with indirect methods or lack of precision due to small sample size in field-based studies. Energetics models often underestimate actual kill rates by large carnivores (Peterson and Ciucci 2003), and classification success of clustering models remains far from perfect (Webb et al. 2008), yielding reasonable estimates of kill rate only over long monitoring intervals and under circumstances where false positives and false negatives at individual location clusters cancel appropriately (Chapter 2). Some inconsistencies might be due to different ecological conditions among regions, but it is currently impossible to ascertain how much of the variation among studies can be ascribed to ecological vs. methodological differences. I believe that visiting GPS telemetry clusters in the field and using a ratio estimator to calculate kill rate represents the current gold standard in kill rate estimation for cougars (see reliability of results below) and future studies using similar techniques in other places will help better define the natural range of variation in cougar kill rate.

Influence of Season

Ungulate kill rate (frequency) increased by a factor of 1.5 during summer when cougars focused predation on smaller juvenile prey. This pattern is similar to that discovered by Sand et al. (2008) for wolves in Scandinavia, and fails to support hypotheses predicting lower kill rate for large carnivores in summer (e.g., Hornocker 1970, Murphy 1998, Laundré 2008), which have led ecologists either to ignore seasonal differences in predation rates (Ballard et al. 1997, Laundré 2005, Varley and Boyce 2006, Laundré et al. 2006) or to assume that predation rates will be highest in winter (White and Garrott 2005, Stahler et al. 2006). Conversely, my results support the hypothesis that frequency of ungulate killing will increase in tandem with the pulse in neonate availability in early summer (Nowak 1999, Laundré 2008, Sand et al. 2008). This seasonal effect must be considered when estimating annual predation rates for ungulate populations subject to cougar predation.

There are three reasons why similar seasonal patterns should be expected for all large carnivores occupying systems where ungulates exhibit a synchronized birth pulse. First, the ungulate birth pulse increases the density of prey available to a predator, which is expected to influence the functional response of un-satiated predators by increasing the probability of encounter (Holling 1959). Second, in contrast to Nilsen et al.'s (2009) claim that roe deer fawns are invulnerable to predation by Eurasian lynx (*L. lynx*), most research indicates that ungulate neonates are highly susceptible to large carnivore predation (Fitzgibbon 1990b, Testa et al. 2000, Mech and Peterson 2003). Third, even if predators are satiated, handling times decrease when smaller prey are incorporated into the diet, resulting in a higher frequency of killing (Holling 1959). Some studies may have failed to identify higher kill rates for large carnivores in summer because methods in those studies did not permit researchers to locate many neonates, or because sample size was too small (Jedrzejewski et al. 2002, Cooley et al. 2008, Nilsen et al. 2009).

Influence of Demography

Age-sex and reproductive class substantively influenced cougar predation patterns. Consequently, cougar population structure should be considered when investigating cougar-ungulate dynamics. Females with kittens displayed the highest frequency of predation, and although my results support the general consensus that family groups have higher kill rates than solitary cougars (Table 1), I did not find a pronounced increase in predation until kittens were older (i.e., >6 months), probably as a consequence of higher energetic requirements of larger kittens. Sub-adults, on the other hand, consistently killed less often, relied more heavily on non-ungulate prey, and killed lower total biomass of prey than adults, supporting Murphy's (1998) hypothesis that experience is an important driver of cougar kill rate. Counter-intuitively, I found that adult males killed ungulates less often than did smaller adult females, but this unexpected result is explained by the larger size of prey killed by males. A focus on large ungulates might also explain why adult males in west-central Alberta killed less often than has been reported for males in other places where fewer species of large prey were available (Table 1). In some cases, therefore, kill rate comparisons might be most usefully made by comparing biomass, especially when comparing between sexes or among studies where the size of available prey differs.

Dietary segregation appears to be common in sexually dimorphic vertebrates (du Toit 2005, Breed et al. 2006), including cougars (Ross and Jalkotzy 1996, Murphy 1998, Anderson and Lindzey 2003). Presumably, a higher proportion of large ungulates in male cougar diet occurs because larger male body size reduces risks associated with attacking larger prey (Sunquist and Sunquist 1989, Iriarte et al. 1990). Yet, larger male body size does not explain why large prey should dominate male diets in systems where deer remain the most abundant prey, such as west-central Alberta (Webb 2009, Chapter 5). A possible alternate explanation is that high intra-specific competition for deer with females increases the value of larger prey for males, which can exploit them more effectively.

Influence of Prey Vulnerability

Cougars in west-central Alberta killed primarily female ungulates just before, during, and after the birthing period (Apr–Jun), male ungulates just before and during the rut (Sep – Nov; Figure 4.4), and juvenile ungulates in spring. This is consistent with the predictions of the reproductive and juvenile vulnerability hypotheses, and reinforces the notion that cougars select for vulnerable prey. Similarly, although cougars are capable of killing prey as large as adult moose and feral horses, prey of this size were rarely taken (<2% of prey weighed >400 kg). Most moose and feral horses killed by cougars (74%) were juveniles, and all cougar age-sex classes killed a higher proportion of large ungulate species (i.e., adults >200 kg) in summer when smaller juveniles were available (Table 3). This pattern is likely due to lower risks associated with attacking smaller prey (Sunquist and Sunquist 1989). Although my seasonal result is novel, the fact that cougar predation on large ungulate species tends to focus on animals <1 year old has been well documented (Hornocker 1970, Turner et al. 1992, Ross and Jalkotzy 1996, Murphy 1998, Husseman et al. 2003).

Although I was unable to distinguish relative contributions of elevated encounter rate (due to increased prey abundance), greater average susceptibility of prey to attack, or greater searching effort by cougars to higher kill rate in summer, these mechanisms were collectively more than twice as important as reduced handling time. Because close grouping between mothers and young (e.g., moose) or hiding behavior of neonates (e.g., white-tailed deer) are strategies that limit searching efficiency during the pulse of juvenile availability in spring (Fitzgibbon 1990b, Fryxell et al. 2007), I suspect that high vulnerability of juveniles to attack when encountered is the dominant force driving elevated summer kill rates.

That vulnerability to attack might influence cougar predation runs contrary to the assumption that that felids kill prey as encountered (Wilmers et al. 2007). Rather, my results support studies indicating widespread selection for vulnerable prey in felid-ungulate systems (Pierce et al. 2000, Molinari-Jobin et al. 2004, Owen-Smith 2008). These patterns can be interpreted as part of a broader optimal foraging strategy (Owen-Smith 2008, Chapter 3) where felids attempt to minimize risks associated with predation by targeting easier prey (Ross et al. 1995, Logan and Sweanor 2001).

Accuracy of Results

Three sources of bias in my GPS telemetry technique might have influenced my results. First, although probably rare, predation events might be missed because a cluster failed to form (in one case in BNP a field crew snowtracked into a kill that was cached in a cave and no cluster was produced). Second, my cluster technique was designed to find prey >8 kg (Chapter 2) and prey less than or close to this size might be missed because handling time is too short to produce a cluster or because I did not locate remains at a cluster where prey was consumed (in some cases only a few tufts of hair and small bone fragments were all that remained of neonate kills). These sources of error would cause me to underestimate kill rate, especially in early summer when ungulate neonates dominated the diet. A third source of error might occur if I classified scavenging events as kills, inflating kill rate estimates and altering prey composition (Chapter 3). Scavenging at kills freshly made by other cougars can be especially difficult to identify, and this almost certainly occurred occasionally (I documented 4 cases of kill sharing by collared cougars with overlapping home ranges). On the other hand, I was able to identify scavenging events on numerous occasions (Chapter 3) and I have no reason to suspect that this source of error would be large enough to substantially alter my conclusions.

Overall, the GPS telemetry approach I used had potential biases similar to radiotelemetry studies where researchers wait until carcasses are consumed before investigating predation sites, but my approach generates far more data. Moreover, potential biases associated with visiting telemetry clusters are fewer than those associated with estimating kill rate using models alone (Chapter 2). Snowtracking can provide more detailed information, but logistical constraints restrict sample size and limit monitoring to winter. Consequently, my approach provides the best balance of accuracy and efficiency of currently available methods.

MANAGEMENT IMPLICATIONS

Predator-prey population models can make predictions to facilitate conservation and management in large mammal communities (Weclaw and Hudson 2004, Lessard et al. 2005, Laundré et al. 2006, Varley and Boyce 2006). The utility of such predictions, however, is limited by the quality of parameter estimates used in the model. The data I provide on cougar kill rate and the influence of season, demography, and prey vulnerability on cougar predation patterns can be applied to better interpret and anticipate cougar-ungulate dynamics.

My results also have application for harvesting cougars to manage ungulate populations. Shifts towards a younger age structure or reductions in the proportion of females rearing kittens in hunted cougar populations (e.g., Stoner et al. 2006, Robinson et al. 2008) can reduce predation rates on ungulates, even if cougar density does not change, because sub-adults have lower kill rates than adults and females without kittens have lower kill rates than those with kittens. Likewise, changing the sex ratio of cougar populations via harvest (e.g., Anderson and Lindzey 2005) might be used to alter the impact cougars have on different species of ungulate in multi-prey systems. Managers should be cautious when applying cougar harvest to enhance ungulate populations, however, because the benefit to ungulates will be situation dependent (Ballard et al. 2001), population-level predator control may not always produce the desired outcome for ungulates (Knopff and Boyce 2007), and side-effects are possible, such as increased conflict with humans when average cougar age is reduced (Lambert et al. 2006).

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CHAPTER 5

PREY SWITCHING, SPECIALIZATION, AND MULTI-SPECIES FUNCTIONAL RESPONSE IN A LARGE CARNIVORE: IMPLICATIONS FOR SMALL POPULATIONS OF ALTERNATE PREY

Predation by generalist predators in multi-prey systems has received substantial attention of late because of its potential to limit small populations of alternate prey at low density and even contribute to extinction (Sinclair et al. 1998, Wittmer et al. 2005, Angulo et al. 2007, DeCesare et al. 2009). However, anticipating the dynamics of such complex multi-species interactions to facilitate management and conservation is challenging. To model the effects predators have on prey, ecologists often multiply the numerical response (number of predators as a function of prey density) by the functional response (number of prey killed per predator as a function of prey density) to determine the total number of prey removed from a population (Solomon 1949, Messier 1995, Hebblewhite et al. 2007). In multi-prey systems, predators can persist and even remain abundant when one or more prey types go to 0, provided other prey are available (i.e., a positive y-intercept in the numeric response to each prey type; Messier 1995). Consequently, the effect generalist predators have on a given prey type in a multi-prey system may depend heavily on the multi-species functional response (MSFR), which describes the rate at which each prey type is killed as a function of the density and relative abundance of all prey (Joly and Patterson 2003, Matthiopoulos et al. 2007).

Depending on the form of the MSFR, a variety of dynamics can ensue (Owen-Smith and Mills 2008). Density independent preference for a particular prey can be destabilizing, resulting in depensatory predation and precipitous declines in the preferred prey (Appendix VII). This is known as asymmetrical apparent competition (DeCesare et al. 2009), and may approach indirect amensalism (0, –) in extreme cases (Chaneton and Bonsall 2000). Equal preference across prey types where prey are killed as they are encountered, on the other hand, produces symmetrical apparent competition, which affects each prey type similarly (–, –). Under these circumstances depensatory predation is less severe (McLellan et al. 2010, Appendix VII), though incidental predation is still thought to present an extinction risk for secondary prey when they are at low abundance (McLellan et al. 2010). Finally, density dependent prey switching where predators avoid prey at low relative abundance and select prey at high relative abundance (Murdoch 1969) creates a de-facto refuge for less abundant prey, facilitating the persistence of small populations of endangered prey (Oaten and Murdoch 1975, Turchin and Hanski 1997, DeCesare et al. 2009).

Although ecologists tend to focus on prey density as the central driver of functional response, a number of additional factors can influence kill rate. Characteristics of the predator such as age, sex, body mass, the size of the group to which it belongs, and reproductive status might be particularly important (Nilsen et al. 2009, Webb 2009, Chapter 4). Indeed, conspecific individuals are rarely ecologically equivalent, and predator-prey models that treat them as such can produce incomplete or even inaccurate understanding of ecological processes (Taylor 1984, Bolnick et al. 2003, Matthiopoulos et al. 2008). Factors associated with the predator's environment such as number of competitors (Abrams and Ginzburg 2000, Jost et al. 2005), weather conditions and season (Stenseth et al. 2004, Sand et al. 2008, Chapter 4), habitat features (James and Stuart-Smith 2000, Hebblewhite et al. 2005), and prey characteristics (Sand et al. 2008, Chapter 4) also might influence kill rate. Accurate prediction of species-specific predation rates in complex natural systems may depend upon incorporating these factors into functional response models (Nilsen et al. 2009, Webb 2009).

Moreover, populations of apparently generalist predators are often composed of individual specialists (Bolnick et al. 2003, Estes et al. 2003). Individual specialization has been identified as a potential driver of dynamics of small populations of alternate prey in multi-prey systems (Festa-Bianchet et al. 2006) and might be an important component of MSFR. Individual specialization takes one of 2 forms. Realized specialization occurs when individuals focus on a particular prey type because their choice of prey is restricted by availability (i.e., prey are selected as available but are heterogeneously distributed across individuals; Bolnick et al. 2003). This is more-or-less identical to the case of symmetrical apparent competition described above and is a predictable function of prey density. In contrast, fundamental specialization arises from phenotypic traits of an individual, such as morphology or behavior, which cause the predator to focus predation on a specific prey type (Bolnick et al. 2003, Estes et al. 2003). Hence, fundamental specialization can be density independent and might be sufficiently difficult to predict that it should be treated as a stochastic process (Festa-Bianchet et al. 2006).

Despite its potential to define prey dynamics in multi-prey systems, MSFRs and their drivers remain poorly understood, chiefly because data required to test assumptions about model structure and to parameterize models are scarce (Gentleman et al. 2003, Garrott et al. 2007). Consequently, ecologists know little about which potential drivers of the MSFR are most important, hampering our ability to predict extinction risk for endangered prey in multi-prey systems. Large carnivores, for instance, are increasingly implicated as a proximate source of species endangerment through asymmetrical apparent competition (DeCesare et al. 2009), but few quantitative assessments of prey switching, prey specialization, or the degree to which predation is predictable or stochastic are available, and MSFR models are seldom fit to empirical data (but see Joly and Patterson 2003, Garrott et al. 2007, and Becker 2008).

Indeed, despite the fact that most large carnivores are generalist predators in multi-prey systems, evaluations of functional response come almost exclusively from simplified single-prey systems (e.g., Messier 1994, Vucetich et al. 2002, Jost et al. 2005, Nilsen et al. 2009). Even where more than one prey species is considered, single species functional response forms still are frequently applied (Dale et al. 1994, Messier 1995, Hebblewhite et al. 2007), although these models almost surely fail to adequately characterize prey dynamics in a multi-species setting (Matthiopoulos et al. 2007, McLellan et al. 2010). Additional empirical data capable of assessing large carnivore MSFR are therefore sorely needed.

I studied the MSFR of cougars (*Puma concolor*) preying on 6 species of wild ungulate in west-central Alberta, Canada. Cougars are important predators of ungulates in North America, and they commonly occur in multi-prey systems where they sometimes function as the proximate source of decline for endangered prey (Logan and Sweanor 2001, Kinley and Apps 2001, Rominger et al. 2004, Gibson 2006). My primary objectives for this chapter were to 1) investigate the prevalence of prey switching and individual specialization in my study population of cougars, 2) identify a mechanistic MSFR model with broad applicability to generalist predators, and 3) distinguish the primary drivers of cougar MSFR using a weight-of-evidence approach and a set of competing models predicting MSFR parameters as a function of the demographic characteristics of individual cougars and features of their biotic and abiotic environment. I discuss my findings in light of the ongoing debate over how best to model large carnivore functional response and the growing need to anticipate and manage the effects of cougars on small populations of endangered prey.

STUDY AREA

My 16,900km^2 study area was located along the eastern slopes of the Rocky Mountains, just east of Banff and Jasper National Parks in west-central Alberta, Canada. Rugged mountains in the western portion of the study area transition to foothills and then to flat boreal mixedwood forests in the east near the towns of Rocky Mountain House and Caroline. Conifer forests were the dominant vegetation and were composed primarily of lodgepole pine (*Pinus contorta)* and white spruce (*Picea glauca*). Intensive logging was ongoing in several portions of the study area, and clearcuts in various stages of regeneration were common. The region supported one of the most diverse large mammal predator-prey assemblages in North America, including elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), feral horses (*Equus caballus*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), the occasional woodland caribou (*Rangifer tarandus*), cougars, wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*U. arctos*). The primary prey of cougars during my study were white-tailed deer, followed by mule deer, moose, elk, feral horses, and bighorn sheep (Chapter 4). Additional details about the flora, fauna, and climate of the region and about the population status and management of cougars in the study area can be found in Chapters 2-4 and Appendix I.

METHODS

Cougar Capture and Collaring

I used data from 37 cougars collared during 2005-2008 with Lotek 4400S GPS collars programmed to obtain a location fix every three hours (Lotek Engineering, Newmarket, Ontario, Canada). I treed cougars using hounds and chemically immobilized them with an intended dose of 3 mg/kg zolazepam-tiletamine (Telazol®, Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and 2 mg/kg xylazine (Rompun®, Bayer, Inc., Toronto, Ontario, Canada) administered via a dart gun (Pneu-Dart Inc., Williamsport, Pennsylvania, USA). Once immobilized, I collared, weighed, measured, sexed, and aged cougars. Age was estimated using a combination of tooth color and wear characteristics (Ashman et al. 1983, Shaw 1986), pelage spotting progression (Shaw 1986), and gum-line recession (Laundré et al. 2000). All cougars were assigned to one of 3 age brackets: kitten (still with mother), sub-adult (dispersal until 2.5-3 yr), or adult (> 2.5-3 yr). My sample consisted of 18 adult females, 5 adult males, 6 sub-adult females, and 8 sub-adult males at capture. Three of the sub-adult females and 2 of the sub-adult males transitioned to adults while they were monitored. All animal handling procedures were conducted under the authority of the Province of Alberta Collection and Research Permit 19872 CN, and were approved by the University of Alberta Animal Care and Use Committee for Biosciences (Protocol # 479505).

Monitoring Cougar Predation

I monitored cougars weekly with radiotelemetry as long as collars were active and attempted to download GPS data every second week. I identified locations where cougars killed prey by visiting clusters of ≥2 GPS locations produced within 200m of each other and within 6 days. Clusters were distinguished using a space-time algorithm (Chapter 2) that allowed me to locate most prey >8kg killed by cougars, including juvenile ungulates and larger non-ungulate prey (Chapter 4). When prey were discovered, I recorded age, sex, and species and estimated the live-weight of prey using averages based on species and age-sex class (Chapter 4, Table 4.2). I monitored predation by individual cougars continuously for an average of 241 consecutive days each (SD = 125 days) and located a total of 1,093 ungulate and 222 non-ungulate predation events. Because non-ungulate prey composition might be biased where animals <8kg were killed by cougars (Chapter 2), and, more importantly, because non-ungulate prey made up a very small portion of the total biomass in cougar diet (Chapter 4) my analyses in this chapter considered predation on ungulates only. I assessed prey composition using the proportion of each prey type in the diet of each cougar and calculated kill rate for each prey type for each cougar by dividing the number of individuals killed by the number of days monitored (Chapter 4).

Prey Density

Obtaining data on prey density and relative abundance is central to assessing prey switching, prey specialization, or developing a MSFR. I assessed cougar prey selection and functional response at the third order (Johnson 1980) by estimating prey availability within a 95% minimum convex polygon (MCP) home range, which I developed for each cougar using location data from GPS collars (Appendix V). I used a combination of aerial survey data and habitat-based abundance models developed in a geographical information system (GIS) to estimate absolute density and relative abundance of deer (mule deer and white-tailed deer combined), elk, moose, feral horses, and bighorn sheep within each MCP.

I estimated densities of deer, elk, moose, and feral horses using a two-step approach. First, linear regression models were developed from 372 1km×2m pellet group strip transects surveyed during 2004-2007 to estimate a pellet-group density index at 30x30m pixels for each species across the entire study area. Starting locations for each transect were placed systematically throughout the study area to ensure adequate coverage. Surveys were conducted immediately after snowmelt (May-July) and so reflect ungulate distribution and abundance during winter (Huggard 1993). Ungulate populations do not exhibit large scale migration in west-central Alberta, except for elk at Ya Ha Tinda, where migratory behavior is declining (Hebblewhite et al. 2006). Consequently, relative abundance probably changed little in summer at the scale of cougar home ranges, although densities increased with the arrival of juveniles.

Methods used for model development and model selection along with the variables retained in the top models used to predict pellet densities for each of the 4 ungulate species are described in detail in Webb (2009). The models did not predict pellet group numbers especially well at small scales (i.e., 5-fold cross-validation correlation coefficients < 0.37 at the level of 30×30m pixels), but produced reasonable estimates of relative abundance at larger scales (e.g., at the scale of large carnivore home ranges; Webb 2009). Model scores for each species were calculated for each cougar's home range by summing the scores of all pixels within the home range.

After model development, elk and moose pellet group abundance scores in each home range were converted into actual densities of animals using aerial survey data. Webb (2009) developed a ratio between the total model score for elk and moose (i.e., summing the scores for all 30x30m pixels) within a provincial Wildlife Management Unit (WMU) and the known densities of elk and moose within WMUs for which density had been estimated during aerial surveys conducted by provincial Fish and Wildlife agency staff in March 2005. The result is the number of animals/unit model score. Model scores for deer and feral horses were transformed into densities by calibrating them against moose densities using defecation rates for each species in a formula adapted from Webb (2009):

$$N_i = \left(\frac{M_i}{C_{moose}}\right)\left(\frac{D_{moose}}{D_i}\right) \qquad \text{Equation 5.1}$$

where N_i is the number of species i (deer or horses), M_i is the total pellet group model score for species i summed over a cougar's home range, C_{moose} is the calibrated number of units of moose model score/moose based on aerial surveys, D_{moose} is the defecation rate of moose, and D_i is the defecation rate of species i. Following Webb (2009), I used a defecation rate of 14 pellet groups/day for moose (Joyle and Ricard 1986, Persson et al. 2000) and 9.7 groups/day for horses (Tyler 1972).

However, I diverged from the approach taken by Webb (2009) to calculate deer densities, using a deposition rate of 22 pellet groups/day instead of 33. Deer defecation rates presented in the literature are highly variable (Neff 1968, Collins and Urness 1981, Rollins et al. 1984, Rodgers 1987, Sawyer et al. 1990), and Webb (2009) used a value at the higher end of the range, possibly resulting in underestimates of true deer densities. Collins and Urness (1981) obtained defecation rates of 22 groups/day in summer for free ranging mule deer in lodgepole pine and aspen (*Populus tremuloides*) forests along the Rocky Mountains in Utah, and expected deposition rates to be much lower in winter. However, Rodgers (1987) found that free ranging white-tailed deer deposited pellet groups at a rate of 22 groups/day in late winter. I felt justified, therefore, in using a rate of 22 groups/day. Indeed, the lower defecation rate I applied may still yield conservative deer densities since it is higher than expected for wild deer in Rocky Mountain ecosystems in winter (Collins and Urness 1981) and higher than most captive studies of deer (Neff 1968, Rollins et al. 1984).

Provincial Fish and Wildlife agency staff estimated bighorn sheep numbers on known winter ranges throughout the study area during 2007 by counting sheep observed on each range during aerial surveys. Based on known numbers of marked sheep tagged as part of an ongoing study at Ram Mountain (Jorgenson et al. 1997), however, only about 60% of all sheep present are located during aerial surveys (C. Feder, Alberta Sustainable Resource Development, Personal Communication). I corrected for this bias by dividing each winter range population count by 0.6. Ground counts of sheep herds on winter ranges where no sheep were counted from the air were used to supplement aerial survey data. I assumed sheep were distributed evenly across winter ranges and I calculated the number of bighorns in each cougar's home range by determining the proportion of each bighorn sheep winter range overlapped by the home range of the cougar, multiplying each of these proportions by the number of sheep on the appropriate range, and summing the totals.

Prey Switching

Density-dependent prey switching occurs when the predator selects a given prey type when relatively abundant and kills fewer than expected when relatively scarce (Murdoch 1969). To test for the presence of switching in a predator population, therefore, prey selection must be evaluated against the relative abundance of each prey species. A specialist predator selects for its prey of choice regardless of relative abundance, a perfect generalist selects prey as available, and a switching predator demonstrates a positive relationship between selection and relative abundance (Figure 5.1).

I estimated selection by individual cougars (*i*) for each prey type (*j*) using Manly's preference index (Manly et al. 1972, Chesson 1983):

$$\alpha_{ij} = \frac{\frac{p_{ij}}{q_{ij}}}{\sum_{j=1}^{n}\left(\frac{p_{ij}}{q_{ij}}\right)} \qquad \text{Equation 5.2}$$

where p_{ij} is the proportion of the j^{th} resource used by individual i and q_{ij} is the proportion of the jth resource category ($j = 1, 2, 3, \ldots, n$) available with the i^{th} individual's home range. When using Manly's preference, values are constrained between 0 and 1 and selection occurs when $\alpha_{ij} > 1/n$ and avoidance when $\alpha_{ij} < 1/n$. Manly's preference is ideally suited for assessing switching because, unlike some other preference indices, it does not change with prey density unless predator behavior changes, permitting comparison across a density gradient (Chesson 1983). Moreover, it has the advantage over methods such as Murdoch's (1969) selection coefficient, which has recently been advocated to assess large carnivore switching behavior (Garrott et al. 2007), of being capable of dealing with more than 2 species simultaneously.

However, where n is greater than 2, comparing the magnitude of selection and avoidance is no longer intuitive. Moreover, where n varies among individual predators, the value at which resources are used as available also varies, rendering α_{ij} incomparable among individuals. To address these problems, I calculated an adjusted measure of selection, X_{ij}, by subtracting $1/n$ from α_{ij} and dividing the result by $1 - \frac{1}{n}$ if positive and $1/n$ if negative. This scaled all selection values between -1 (perfect avoidance) and 1 (perfect selection), where 0 represents use as available. I then plotted selection (X_{ij}) against relative abundance (q_{ij}) to test for the presence of prey switching in my study population of cougars.

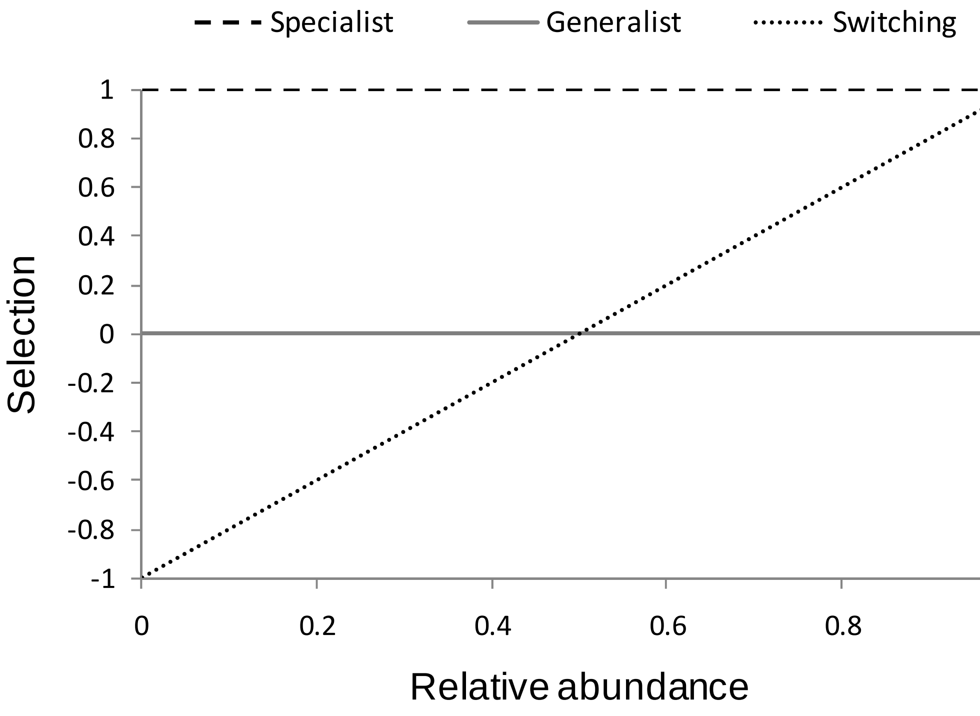

Figure 5.1: Conceptual relationship between the relative abundance of prey and selection for prey by perfect specialist, perfect generalist, and switching predators. Selection is given on a scale of 1 to -1, where 0 represents use as available.

Prey Specialization

Although previous studies have suggested that individual cougars specialize on certain prey types (Ross et al. 1997, Knopff and Boyce 2007), and this behavior has been implicated as a driving force underlying extinction risk in small ungulate populations subject to cougar predation (Festa-Bianchet et al. 2006), the prevalence of specialist predation in cougar populations has not been assessed. Moreover, no study has simultaneously provided data on prey composition and home-range scale prey availability to test whether cougar specialization is realized or fundamental.

To determine whether apparently generalized foragers, such as cougars (Iriarte et al. 1990, Murphy and Ruth 2009, Chapter 4), are in fact composed primarily of individual specialists, Bolnick et al. (2002) advocated one of 2 related indices to quantify resource overlap between each individual organism and its population. The first, PS_i, is calculated using

$$PS_i = 1 - 0.5\sum_j |p_{ij} - q_j| \qquad \text{Equation 5.3}$$

where p_{ij} is the proportion of the jth resource used by individual i and q_j is the proportion of the jth resource category in the population's niche. The second, W_i, takes the form

$$W_i = \left(\prod_j \left(\frac{q_j}{p_{ij}}\right)^{n_{ij}}\right)^{1/n_{i\bullet}} \qquad \text{Equation 5.4}$$

where p_{ij} and q_j are the same as above, n_{ij} is the number of diet items in individual i's diet that fall in category j, and $n_{i\bullet}$ is the number of diet items used by individual i.

Such approaches can be useful for identifying whether individual predators use only a subset of the total niche breadth exhibited by the population and may provide insight into population level prevalence of specialization in some cases. Because they do not incorporate information on resource availability, however, they cannot distinguish between fundamental and realized specialization. To discriminate between types of specialization, I developed an index based on Manly's preference (equation 5.2) capable of quantifying the degree of individual specialization relative to availability where multiple species of prey are present. The index combines the Manly's preference scores for each prey type to produce a Standardized Specialization Index (SSI) for multiple prey systems:

$$SSI_i = 1 - \frac{\sum_{j=1}^{n}\sqrt{\left(\alpha_{ij} - \frac{1}{n}\right)^2}}{2\left(1 - \frac{1}{n}\right)} \qquad \text{Equation 5.5}$$

where n is the number of prey types available to individual i, $1/n$ is the Manly's preference score when prey are used as available, and α_{ij} is the observed Manly's preference for each of j prey species for individual i. When all prey items are consumed according to availability, the numerator in the fraction goes to 0 and the denominator ensures that when only 1 prey type is consumed in a multi-prey system the fraction goes to 1. By subtracting this fraction from 1, the SSI yields values on the same 0 to 1 scale as PS_i and W_i, where a pure generalist obtains a value of 1 and a pure specialist obtains a value of 0.

I calculated all three indices (PS_i, W_i, and SSI_i) for ungulate prey divided into 5 categories (deer, moose, elk, bighorn sheep, and feral horse) to evaluate the prevalence and nature of individual specialization in cougars in west-central Alberta. To minimize bias in prey composition estimates associated with shorter monitoring periods (Chapter 2), individuals included in this analysis were all monitored for >70 consecutive days. Where specialization was identified, I considered cougars to specialize primarily on a single prey species if that species contributed ≥65% of the biomass in the cougar's diet and if X_{ij} for that species was ≥0.4, indicating strong selection. I used table 4.2 (Chapter 4) to assign biomass to each prey item when calculating the proportion contributed by each species to an individual's diet.

Functional Response Modeling

Prey-Dependent vs. Ratio-Dependent

Despite theoretical importance and persistent use, Holling's (1959a) classic prey-dependent functional response forms (i.e. Type II and III) rarely characterize large carnivore kill rate well (Marshal and Boutin 1999, Hayes and Harestad 2000, Vucetich et al. 2002, Nilsen et al. 2009, Webb 2009). Ratio-dependent functional responses, where kill rate reflects the ratio of predators to prey, have been used instead because they tend to fit available data better (Vucetich et al. 2002, Jost et al. 2005, Garrott et al. 2007). Yet, many researchers hold firmly to the prey-dependent approach because they cannot reconcile the peculiar dynamics of ratio-dependent models (Abrams 1994, Messier and Joly 2000, Varley and Boyce 2006). No clear resolution to this debate has been forthcoming and both types of models continue to be applied (Varley and Boyce 2006, Garrott et al. 2007).

The lack of consensus may matter little, however, because both approaches are oversimplified (Abrams and Ginzburg 2000, Schenk et al. 2005), especially for large carnivores where a diversity of factors in addition to prey density and predator interference are known to influence kill rate (Hayes et al. 2000, Sand et al. 2008, Chapter 4). Researchers have recently advanced a new approach that incorporates a variety of potential drivers of kill rate as covariates underlying variation in the parameter values of traditional prey-dependent functional response models (Nilsen et al. 2009, Webb 2009). In theory, either ratio- or prey-dependent models can provide the underlying model structure, but in practice using a prey-dependent model and incorporating predator interference as a covariate for one or more parameters accommodates the mechanism behind ratio-dependence without the drawbacks associated with traditional ratio-dependent model forms (Abrams 1994, Appendix VI).

Incorporating drivers other than prey density into functional response models has two important advantages. First, it permits variation in predation patterns by predator sex, reproductive status, age, group size, and the environmental conditions to which the predator is exposed (Nilsen et al. 2009, Webb 2009). Second, it provides a framework to test hypotheses about which of these factors are the most important drivers of kill rate (Nilsen et al. 2009, Webb 2009). I therefore abstained from applying either strictly prey- or ratio-dependent models and chose instead to extend the more flexible third approach to a multi-species context and use it to explore drivers of cougar MSFR.

A general model for MSFR

A MSFR simultaneously outputs kill rates for each of several prey types. To be biologically reasonable, the model must meet some basic requirements. First, a predator cannot consume prey when none are available, hence kill rate for a given prey type must go to 0 when the density of that prey goes to 0. Second, satiation is common if not universal in large carnivores and so must be incorporated into the model (Jost et al. 2005, Nilsen et al. 2009). Third, satiation cannot be independent for different prey, and time spent handling prey of one type must reduce the time available to kill and consume other prey types (McLellan et al. 2010). A simple MSFR modified from Holling's (1959b) disc equation that meets each of these criteria is given by McLellan et al. (2010):

$$Y_t = \frac{A\sum_{j=1}^{n} N_j}{1 + A\left(\sum_{j=1}^{n} N_j\right)T_h} \qquad \text{Equation 5.6}$$

where Y_t is the combined number of all n prey killed per predator per unit time, A is the rate of effective search (km^2/unit time), N_j is the density of the j^{th} prey type, and T_h is the time to handle 1 prey. Kill rate for each species (Y_j) can be calculated by multiplying Y_t by the relative abundance of the j^{th} prey. McLellan et al. (2010) used this model to evaluate the potential for predator-mediated Allee effects in caribou subject to large carnivore predation in a multi-prey system.

However, the McLellan et al. (2010) model is limited in at least 2 important respects. First, it assumes that all prey types are of equal size and require the same amount of time to handle, which is clearly untrue in many multi-prey systems. Second, as with most disc-equation models, it assumes prey are killed as they are encountered. Consequently, diet is directly proportional to availability (i.e., predators are perfect generalists) and the probabilities of attack given an encounter and kill given an attack cannot vary among prey types to accommodate switching, specialization, or other factors that cause predators to select some prey over others. To address these limitations, McLellan et al.'s (2010) model can be adjusted in the following way:

$$Y_t = \frac{A\sum_{j=1}^{n} P_j N_j}{1 + A\sum_{j=1}^{n} \frac{P_j N_j M_j}{C}} \qquad \text{Equation 5.7}$$

where Y_t, A, and N_j are the same as above, P_j is the predator's preference for the j^{th} prey type (a value from 0-1 reflecting the combined probabilities of attack given encounter and kill given attack), M_j is the average mass of the j^{th} prey type (kg), and C is the consumption rate expressed as kg/unit time. When considered together, M_j/C gives the handling time in units of time/prey. This formulation is structurally similar to the MSFR given by Joly and Patterson (2003). Species specific kill rates are calculated using:

$$Y_j = Y_t \left(\frac{P_j N_j}{\Sigma_1^n (P_j N_j)} \right) \qquad \text{Equation 5.8}$$

To incorporate other drivers of kill rate into the MSFR, the parameters A, C, and P_j all can be allowed to vary as a function of a series of covariates (Joly and Patterson 2003, Nilsen et al. 2009). The covariates chosen will depend on the specific questions asked by the investigator and prior knowledge of the system being investigated. One covariate that should almost certainly be considered is prey density. Indeed, Abrams (1990) argues that constant-parameter functional response models will fare poorly at prediction precisely because they fail to account for possible adaptive responses in search rate and handling time as a function of prey density. This is especially important when investigating P_j. Although equation 5.7 dictates that Y_t always follows a type II functional response, density dependent responses in P_j (prey switching) can reduce predation rates for prey at lower relative abundance, producing dynamics similar to a type III functional response for Y_j under certain conditions (Joly and Patterson 2003).

Fitting the model

Season has a substantial influence on cougar predation (Chapter 4) and extreme differences in size, behavior, and vulnerability of adult vs. neonate ungulates in summer makes it appropriate to classify them as separate prey. To keep my analysis manageable, I therefore parameterized equation 5.7 using data from winter only (15 Oct – 14 Apr). I also only used data from monitoring periods where cougar age, sex, and reproductive class (no kittens [NK], kittens <6 months [K<6], or kittens >6 months [K>6]) remained constant. Where cougars transitioned among classes, I selected the class with the longest monitoring period for each individual cougar. This left me with a subset of 35 cougars (7 AFNK, 9 AFK>6, 2 AFK<6, 6 AM, 6 SAF, 5 SAM) for which I monitored within class predation continuously for an average of 104 winter days each (SD = 45). I modeled variation in A, C, and P_j independently using these data.

Efficiency and Satiation

I began by considering A, which is often thought of as an efficiency parameter because it defines how quickly the predator reaches satiation as prey density increases from 0. Large carnivores are efficient predators, reaching asymptotic kill rate values at low prey density and are saturated across most of the density range (Dale et al. 1994, Hayes and Harestad 2000, Nilsen et al. 2009). Consequently, it may be difficult or impossible to model A if data at low prey densities are unavailable and the predator is already satiated (i.e., kill rate no longer increases as a function of prey density).

I tested for satiation across the range of prey density available to cougars in west-central Alberta by regressing Y_t (no. ungulates/day) against prey density (no. ungulates/km^2) using each cougar as the sample unit. I predicted the slope of the line to be nearly flat if cougars were satiated and expected a steeper positive slope if cougars were not satiated over at least part of the available range. I used multiple regression to control for the effects of, age, sex, average size of prey items consumed by the cougar, and cougar body mass (including mass of dependent kittens; see Chapter 4 for calculation methods), all of which can influence Y_t (Chapter 4) and may do so independent of prey density. Here, as in all regression analyses in this chapter, I avoided multicollinearity problems by excluding combinations of variables correlated at $|r| > 0.7$ from the same model.

Although large carnivores commonly achieve satiation (Messier 1994, Hayes and Harestad 2000, Webb 2009, Nilsen et al. 2009), they rarely spend all of their time physically handling prey, which is the usual mechanism thought to determine satiation (Holling 1959b). Cougars in west central Alberta, for instance, spent only 42% (SD = 14%) of their time at location clusters where I found an ungulate predation event, but were apparently satiated (see results). Where this mismatch occurs, satiation must be considered broadly, incorporating additional factors such as the time it takes to pursue, subdue, and digest prey (Holling 1966, Abrams 1990). In particular, where predation poses a risk to the predator, as it does for large carnivores preying on ungulates (Ross et al. 1995, Logan and Sweanor 2001, Murphy and Ruth 2009), the time it takes for the predator to become hungry enough for the benefits of predation to outweigh the risks might also play an important role in satiation.

To test this hypothesis, I partitioned the intervals between consecutive ungulate kills into the time spent physically handling prey and the time it took the cougar to kill a second ungulate after leaving the carcass of the first (i.e., search time; see Chapter 4 for additional detail). I compared data for females without kittens, females with kittens <6 months and females with kittens >6 months separately for summer and winter. If trading off the risks and benefits of predation plays a role in cougar satiation (H_1), I expected not only time spent at carcasses to decline with the presence of kittens, but "search" times also would become shorter because increased caloric demands of kittens would reduce the amount of waiting time before the benefits of predation outweigh the risks. Otherwise (H_0), I expected reductions in time spent at a carcass to account for most of the increase in kill rate I previously observed when females have kittens (Chapter 4).

Because I found strong evidence for satiation in my sample of cougars (see results), I was unable to model variation in *A* and therefore assigned a fixed value instead. The relationship between kill rate and prey density was negative across the range of prey densities I measured (see results), and consequently a maximum likelihood approach to estimating *A* from equation 5.7 (a Type II curve) would attempt to assign an infinitely large value. I therefore assigned what I believed to be a biologically reasonable value that still produced rapid satiation by cougars (i.e., $10 km^2/day$, see results). This does not mean that cougars must physically search an area of this size each day; rather, it indicates that they can encounter prey occurring within that area (possibly because they know where to find them; McPhee 2009).

Consumption Rate

In equation 5.7, the predator becomes satiated when all of its time is spent consuming prey and is determined by the value of the consumption rate (*C*). Because cougars in west-central Alberta were satiated with respect to prey density (see results), I was able to obtain empirical estimates of *C* for each cougar by dividing the total kilograms of prey it killed by the number of monitoring days during winter. I then modeled *C* using a Generalized Linear Model (GLM) with a Gaussian distribution and an identity link in STATA 10 (StataCorp, College Station, Texas, USA). I developed a suite of candidate models in a multiple working hypothesis framework and used the small sample size correction for Akaike's Information Criterion (AICc) to assess the weight of evidence for each model (Burnham and Anderson 2002). Covariates in the different models included total prey density (N_t) in each cougar's home range, physical characteristics of cougars such as sex, age, and total cougar mass (including weight of dependent kittens), and environmental characteristics such as proportion of edge habitat, density of linear features, and average terrain ruggedness, which I calculated within each cougar's 95% MCP using a GIS.

Preference

Chesson (1983) showed that Manly's preference index can be interpreted as the relative probability that each prey type would be killed if it were encountered. Unlike other preference indices, therefore, Manly's index should predict the relative quantities of each prey type killed after accounting for availability (assuming prey are encountered randomly). Applying Manly's preference to a MSFR is an approach first advocated by Joly and Patterson (2003), and I followed suit. Statistical models capable of investigating the drivers of P_j must consider the fractional nature of the response variables (i.e., $1 \leq P_j \geq 0$ and all P_j sum to 1). In their seminal work, economists Papke and Wooldridge (1996) showed how to do this using a Bernouilli quasi-maximum likelihood estimator. However, this model restricts the analysis to only 2 outcomes, which is why Joly and Patterson (2003) suggest that modelling Manly's preference is only possible when the prey of interest are considered against all other prey combined. Recently, however (again thanks to economists), fractional response regression has been extended to the multinomial case where more than 2 prey can be considered simultaneously (http://www.maartenbuis.nl/software/fmlogit.html).

To assess the underlying drivers of cougar preference I used Manly's preference scores for each prey type for each cougar (equation 5.2) as my response variables and modeled these as a function of a series of covariates using the fmlogit command in STATA (http://www.maartenbuis.nl/software/fmlogit.html). This model cannot accommodate missing data, and because bighorn sheep were unavailable in 63% of cougar home ranges (i.e., Manly's preference for sheep could not be calculated for these individuals) I was forced to drop bighorns as a prey type. This also meant excluding the

1 cougar that killed bighorns during winter from this analysis and from subsequent model evaluation (see below). Consequently, my analysis of preference considered only deer, elk, moose, and feral horses and my sample consisted of 34 cougars. Just as I did for consumption rates, I developed a set of candidate models and selected among them using AICc. Covariates in the different models were the same as those used for consumption rates except that I used the density and relative abundance of each prey type instead of total prey density.

Model Evaluation

I first evaluated the structure of equation 5.7 by fitting it for each cougar (i) using the fixed value for A, and the values for C_i (kg/day), P_{ij} (Manly's preference for each prey for each cougar), M_{ij} (average size for each prey species for each cougar), and N_{ij} (density of each prey in the home range of each cougar) estimated in the field. I calculated Y_{ij} using equation 5.8 and compared these values to the raw kill rate data for cougars using a linear regression. A correctly structured model should predict Y_{ij} perfectly, resulting in a regression with an intercept of 0, a slope of 1, and an R^2 of 1.

Next, I assessed the overall predictive ability of the MSFR by incorporating the models with the highest AICc score for C and P_i into equation 5.7, yielding a complete MSFR for cougars. A was assigned a fixed value of 10km^2/day, M_i were assigned the average weights of each prey type recorded at winter predation events during my study (deer = 60kg, elk =194kg, moose = 288kg, feral horse = 362kg), and N_i was calculated from the 95% MCP of each cougar. I evaluated the fit of the MSFR by calculating an R^2 value for the relationship between observed and predicted values for each species.

RESULTS

Prey Switching

Cougars tended to select for prey at high relative abundance and avoid prey at low relative abundance ($R^2 = 0.37$, $P < 0.001$), consistent with prey switching as defined by Murdoch (1969). Deviations from a strict switching pattern were not uncommon, however (Figure 5.2). Because deer were always the most abundant prey in all cougar home ranges, it was difficult to distinguish clearly between prey switching and density independent preference for deer over other ungulates. When each prey type was considered independently, however, the positive relationship between relative abundance and selection persisted in most cases: deer (slope = 2.36, *P* = 0.080), elk (slope = -5.9, *P* = 0.042), moose (slope = 2.17, *P* = 0.208), feral horse (slope = 2.32, *P* = 0.119), bighorn sheep (slope = 7.37, *P* = 0.055).

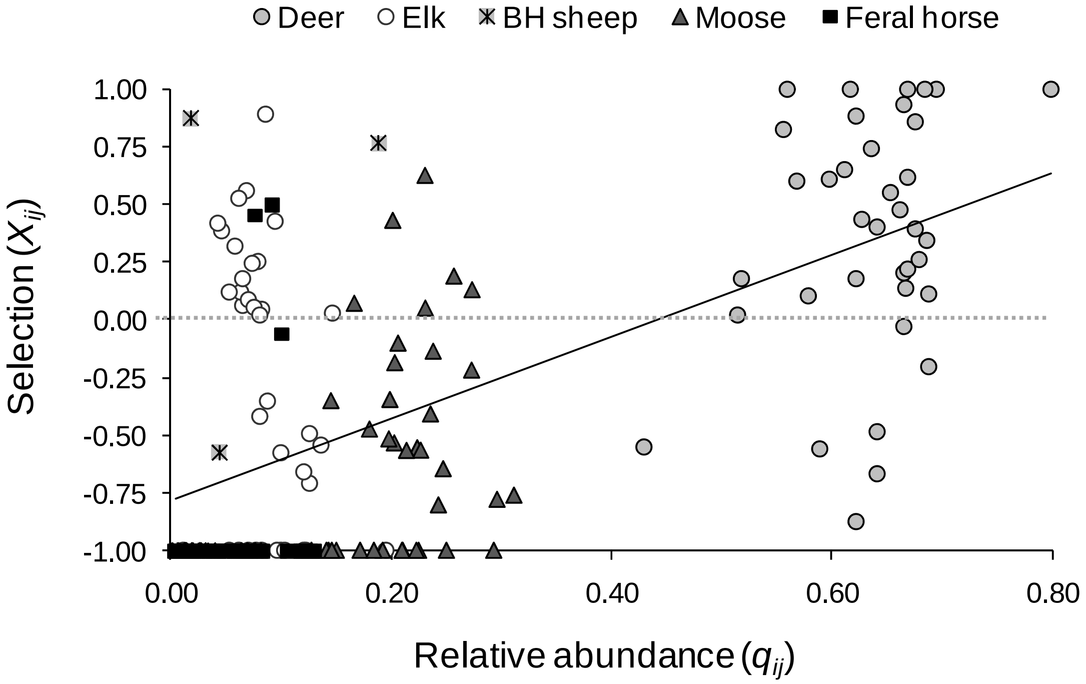

Figure 5.2: Selection for 5 types of ungulate prey as a function of relative abundance at the home range scale by 37 cougars in west-central Alberta during 2005-2008. The black line represents the best fit least-squares regression through the data and the dotted line indicates use as available.

Prey Specialization

Scores for PS_i and W_i were similar to one another and revealed that some individuals, most notably 0110R, 9827R and 9829R, exhibited niche width substantially less broad than the population niche (Table 5.1), indicating specialized foraging according to the criteria of Bolnick et al. (2002). However, most PS_i and W_i scores pointed to substantial overlap between the niche expressed by individual cougars and that of the population, indicating generalized predation with mean values of 0.80 (SD = 0.17) for PS_i and 0.79 (SD = 0.22) for W_i (Table 5.1). When I calculated SSI_i, on the other hand, specialist predation by individuals emerged as the dominant pattern (Table 5.1). Few cougars ($n = 4$) exhibited SSI_i scores consistent with generalized predation (i.e., >0.5), and the population average was 0.31 (SD = 0.20).

In only 2 cases (9878R and 9881R) was a cougar's primary prey (i.e., greatest biomass) avoided or used as available (Table 5.1). All other cougars exhibited selection for their primary prey, and 70% of cougars ($n = 26$) focused predation principally on a single species (Table 5.1). Patterns of specialization differed by age-sex class and 100% of adult male and 33% of sub-adult male single species specialists focused on large prey (e.g., moose, elk, and feral horses where adults weigh >200kg), while female single species specialists always focused on small prey (e.g., deer and bighorn sheep where adults weigh <100kg; $\chi_1^2 = 16.80$, $P < 0.001$). Instances where cougars specialized on species other than deer (Table 5.1) were the source of most of the deviations from a switching pattern (Figure 5.2).

Table 5.1: Specialization index scores and primary prey characteristics for 37 cougars monitored in west-central Alberta during 2005-2008.

Cougar characteristics			**Specialization indices**			**Primary prey characteristics**					
ID	**Age-sex**	**No. kills**	PS_i	W_i	SSI_i	**Species**	**Percent biomass in diet**	**Percent frequency in diet**	**Percent frequency available**	X_{ij}	**Single species specialist**
0003R	SAF	37	0.93	0.95	0.45	Deer	81%	88%	65%	0.55	Yes
0108R	SAF	20	0.93	0.95	0.48	Deer	85%	88%	69%	0.34	No
0110R	SAF	22	0.26	0.06	0.24	BHS	82%	75%	19%	0.76	Yes
0111R	SAM	20	0.90	0.93	0.67	Deer	71%	75%	67%	0.20	No
0112R	AF	25	0.95	0.95	0.48	Deer	65%	83%	67%	0.13	No
0113R	SAM	20	0.90	0.87	0.33	Deer	71%	80%	66%	0.48	Yes
0114R	SAM	20	0.95	0.95	0.53	Deer	79%	80%	67%	0.22	No
0115R	AF	20	0.92	0.95	0.55	Deer	76%	88%	64%	0.40	Yes
9822R	AF	9	0.81	0.81	0.00	Deer	100%	100%	80%	1.00	Yes
9823R	SAF	50	0.86	0.86	0.33	Deer	83%	95%	60%	0.61	Yes
9824R	AF	12	0.81	0.81	0.00	Deer	100%	100%	68%	1.00	Yes
9825R	AF	35	0.85	0.88	0.14	Deer	73%	96%	68%	0.86	Yes
9827R	AM	39	0.32	0.22	0.45	Horse	66%	49%	9%	0.49	Yes
9828R	SAF	17	0.87	0.87	0.25	Deer	72%	93%	63%	0.43	Yes
9829R	AM	7	0.46	0.32	0.11	Elk	80%	60%	9%	0.89	Yes
9871R	AF	63	0.89	0.89	0.48	Deer	85%	90%	68%	0.40	Yes
9873R	AF	117	0.89	0.94	0.40	Deer	85%	92%	57%	0.60	Yes
9875R	AF	7	0.87	0.81	0.33	Deer	64%	83%	69%	0.11	No

9876R	AM	54	0.75	0.80	0.67	Moose	39%	29%	27%	0.13	No
9877R	SAM	18	0.62	0.61	0.45	Moose	76%	47%	20%	0.43	Yes
9878R	AF	59	0.87	0.88	0.48	Deer	55%	72%	67%	-0.03	No
9879R	AF	78	0.86	0.91	0.18	Deer	82%	95%	56%	0.82	Yes
9881R	SAM	12	0.81	0.58	0.13	Deer	87%	80%	64%	-0.48	No
9884R	AF	61	0.91	0.94	0.39	Deer	86%	90%	67%	0.61	Yes
9885R	SAF	51	0.81	0.81	0.00	Deer	100%	100%	56%	1.00	Yes
9886R	SAF	42	0.85	0.88	0.12	Deer	96%	96%	62%	0.88	Yes
9887R	SAM	27	0.79	0.83	0.47	Elk	38%	20%	9%	0.43	No
9888R	AF	51	0.93	0.95	0.49	Deer	72%	84%	68%	0.26	No
9889R	AM	33	0.52	0.48	0.36	Moose	81%	58%	23%	0.63	Yes
9890R	AF	44	0.86	0.86	0.33	Deer	90%	95%	61%	0.65	Yes
9891R	AF	37	0.92	0.95	0.41	Deer	79%	85%	62%	0.17	No
9892R	AF	56	0.90	0.90	0.26	Deer	81%	91%	64%	0.74	Yes
9893R	AF	71	0.83	0.85	0.07	Deer	89%	98%	67%	0.93	Yes
9895R	SAM	5	0.81	0.81	0.00	Deer	100%	100%	69%	1.00	Yes
9896R	AF	32	0.81	0.81	0.00	Deer	100%	100%	67%	1.00	Yes
9897R	AM	33	0.49	0.43	0.48	Horse	65%	31%	8%	0.45	Yes
9898R	AF	11	0.81	0.81	0.00	Deer	100%	100%	62%	1.00	Yes

Functional Response

Efficiency and Satiation

Total prey density in cougar home ranges varied between 0.82 and 2.29 ungulates/km^2 (Figure 5.3). The slope of a regression line fit to the raw kill rate and prey density data was –0.27 (Figure 5.3), but was not significant and explained little of the variation in kill rate ($R^2 = 0.036$, $P = 0.273$). Multiple regression analysis incorporating other covariates known to influence cougar kill rate fit the data well ($R^2 = 0.752$, $P < 0.001$) and produced a coefficient of –0.36 as prey density increased (Table 5.2). Although failure for kill rate to increase at higher prey density indicated satiation, kill rates still varied 16-fold among cougars (Figure 5.3). Satiation appeared to be driven, at least in part, by tradeoffs between the risks and benefits of predation. Not only did handling time decrease for female cougars with kittens, but the time spent "searching" for prey also declined (Table 5.3). This result was consistent across seasons and suggests that females without kittens are capable of increasing their effort to achieve higher kill rates but do not fulfill this potential, presumably because it was to their advantage to spend more time engaged in non-hunting activities between kills. Consequently, the most interesting source of variation in Y_t for cougars may be found in the consumption rate, which allows kill rate at satiation to shift up or down at a given prey density as a function of a series of covariates.

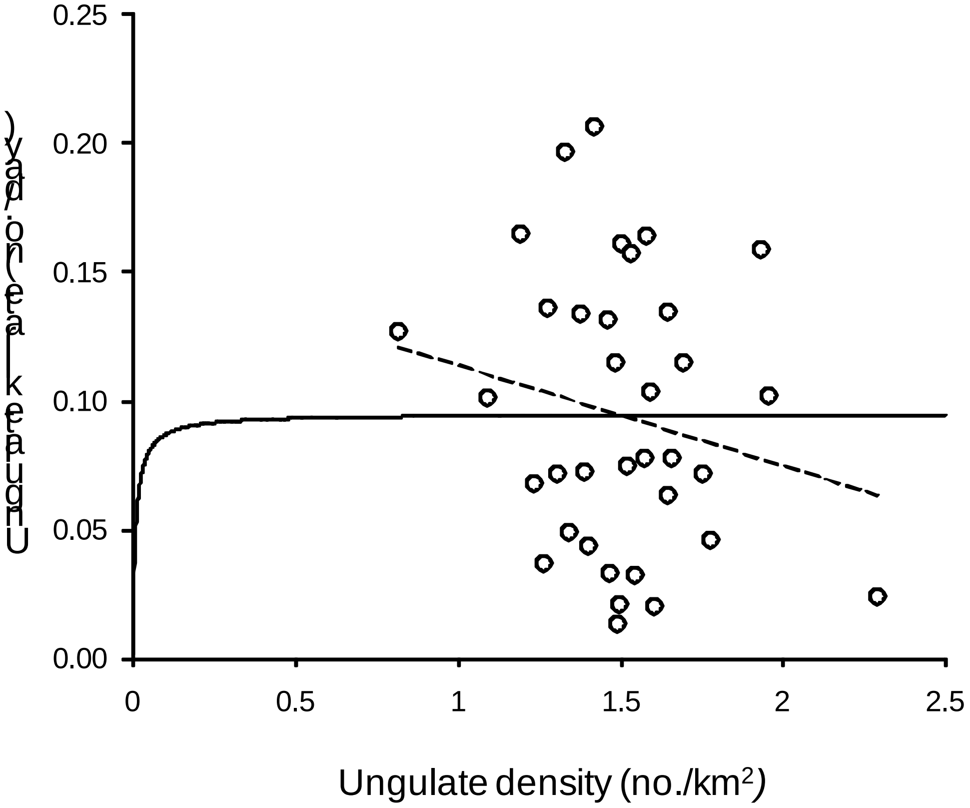

Figure 5.3: The relationship between total kill rate (Y_t) and total prey density (N_t) for 35 cougars in west-central Alberta in winter during 2005-2008. The dashed line is the best fit least squares regression to the data and the solid curve is a type II functional response of the form given in equation 5.7 with all P_i set to 1 and parameters of 10 km^2/day for A and the average handling time of 10.6 days/prey for all M_i/C, which produces satiation at the average winter kill rate of 0.09 prey/day.

Table 5.2: Regression coefficients, standard errors, p-values, and 95% confidence intervals for a linear regression fit to total cougar kill rate (Y_t) for 35 cougars in winter in west-central Alberta during 2005-2008.

Variable	**Coefficient**	**Standard Error**	***P***	**95% Confidence Interval**
age[a]	0.3271	0.0950	0.002	0.1329, 0.5214
sex[b]	-0.0002	0.0929	0.998	-0.1902, 0.1897
cougkg[c]	0.0074	0.0013	0.000	0.0046, 0.0101
preysize[d]	-0.0663	0.0431	0.135	-0.1545, 0.0219
total_d[e]	-0.3570	0.1445	0.020	-0.6525, -0.0614
Constant	0.5692	0.2210	0.015	0.1170, 1.021

[a] Cougar age (A = 1, SA = 0)
[b] Cougar sex (M = 1, F = 0)
[c] Cougar mass (kg) including mass of dependent kittens
[d] Average mass of prey items consumed (kg)
[e] Density of all prey (ungulates/km^2)

Table 5.3: Average time spent by cougars at clusters of telemetry locations where an ungulate prey was found (handling) and between consecutive telemetry clusters associated with ungulate prey during inter-kill-intervals in summer and in winter by female cougars without kittens, with kittens >6 months, and with kittens <6 months in west-central Alberta during 2005-2008.

Season	**Kitten age**	**Handling time (hours)**	**Search time (hours)**	***n***
Summer	No kittens	63^{a}	114^{a}	10
	<6 months	67^{a}	101^{ab}	5
	>6 months	42^{b}	70^{b}	7
Winter	No kittens	84^{a}	260^{a}	14
	<6 months	98^{a}	145^{a}	7
	>6 months	54^{b}	111^{a}	11

Different letters within columns and seasons denote statistically significant differences ($P < 0.1$) identified using a Sidak post-hoc comparison after a one-way analysis of variance.

Consumption Rate

Prey density and habitat variables were unimportant for describing variation in cougar consumption rates at satiation, and the top model included only covariates for physical characteristics of individual cougars (Table 5.4). Indeed, all models that achieved any support (as judged by Akaike weights, w_i) included some combination of age, sex, and cougar size (Table 5.4). The number of kg/day consumed was higher for adults and males than for subadults or females and also increased with total cougar mass (Table 5.5). Together these three covariates explained over 50% of the variation in C ($R^2 = 0.53$).

Table 5.4: Top-ranked linear regression models for cougar consumption rates (*C*) in west-central Alberta, Canada in winter during 2005–2008. The models are shown in order of decreasing rank within each of 5 model suits with log-likelihood (LL), number of estimated parameters (K), small sample size corrected Akaike's Information Criterion (AICc), AICc difference (Δ_{AICc}), and AIC weight (w_i) displayed for each. All covariates are attributed to an individual cougar or its 95% minimum convex polygon (MCP) home range.

Rank	**Variables**	**LL**	***K***	**AICc**	**Δ AICc**	w_i
Prey density						
14	*total_d*[a]	-104.6	1	211.25	20.9	0.00
Environmental characteristics						
13	*ter_rug*[b]	-102.4	1	206.97	16.6	0.00
15	*linear*[c] *edge*[d] *open*[e]	-102.5	3	211.76	21.4	0.00
Physical characteristics						
1	*age*[f] *sex*[g] *cougkg*[h]	- 91.8	3	190.34	0.0	0.62
10	*cougkg*	-101.0	1	204.14	13.8	0.00
Physical & Environmental						
2	*age sex cougkg linear edge open*	- 89.2	6	193.44	3.1	0.13
3	*age sex kittenage edge*	- 92.7	4	194.68	4.3	0.07
6	*age sex kittenage linear edge open*	- 90.7	6	196.40	6.1	0.03
8	*cougkg edge*	- 98.7	2	201.76	11.4	0.00
11	*cougkg linear edge open*	- 98.1	4	205.60	15.3	0.00
Comprehensive						
4	*age sex cougkg edge total_d*	- 91.3	5	194.68	4.3	0.07
5	*age sex kittenage ter_rug open total_d*	- 90.2	6	195.35	5.0	0.05
7	*age sex cougkg linear edge open total_d*	- 89.2	7	196.62	6.3	0.03
9	*cougkg edge total_d*	- 98.5	3	203.86	13.5	0.00
12	*cougkg ter_rug open total_d*	- 98.1	4	205.61	15.3	0.00

[a] Density of all prey

[b] Average terrain ruggedness calculated using a 500m moving window

[c] Kilometers per km^2 of linear features (seismic lines, pipelines, and roads)

[d] Proportion of edge habitat (100m buffer around intersection of forest and open habitat)

[e] Proportion of open habitat

[f] Cougar age (A = 1, SA = 0)

[g] Cougar sex (M = 1, F = 0)

[h] Cougar mass (kg) including mass of dependent kittens

Table 5.5: Coefficients, standard errors, *P* values and 95% confidence intervals for the highest ranked linear regression model used to predict cougar consumption rates (*C*) in west-central Alberta in winter during 2005–2008.

Variable	**Coefficient**	**Standard Error**	***P***	**95% Confidence Interval**
age[a]	5.70	1.47	0.001	2.70, 8.70
sex[b]	4.53	1.33	0.002	1.81, 7.25
cougkg[c]	0.47	0.22	0.043	0.00, 0.09
Constant	-1.10	1.75	0.533	-4.68, 2.47

[a] Cougar age (A = 1, SA = 0)
[b] Cougar sex (M = 1, F = 0)
[c] Cougar mass (kg) including mass of dependent kittens

Preference

The top fractional multinomial regression model describing variation in cougar preference included the same terms for physical characteristics of cougars as the top consumption rate model (i.e., age, sex, and mass). Indeed, physical characteristics of cougars appeared to be the most important drivers of preference, and all models with $w_i >$ 0.1 included cougar age, sex, and mass as covariates (Table 5.6). Just as in the consumption model, the habitat covariates I hypothesized might be important drivers of prey selection contributed little to the variation in P_j (Table 5.6). The top preference model did, however, included a term for the relative abundance of deer (Table 5.6). Although relative abundance and absolute density for each species were always correlated ($R > 0.7$), relative abundance consistently outperformed density as a predictor variable. Hence, with the exception of the density only model for comparison with the relative abundance only model, all results presented here incorporate only relative abundance (Table 5.6). Because densities of feral horses were highly and positively correlated with those of deer ($R > 0.7$), and because relative abundance across all 4 species sums to 1 (i.e., redundant information in one of the 4 categories) horse density and relative abundance were not used in model development.

Table 5.6: Top-ranked fractional multinomial regression models for cougar preference (P_j) for deer, elk, moose, and feral horses in west-central Alberta, Canada in winter during 2005–2008. The models are shown in order of decreasing rank within each of 5 model suits with log-pseudo-likelihood (LPL), number of estimated parameters (K), small sample size corrected Akaike's Information Criterion (AICc), AICc difference (Δ_{AICc}), and AIC weight (w_i) displayed for each. All covariates are attributed to an individual cougar or its 95% minimum convex polygon (MCP) home range.

Rank	Variables	LPL	*K*	AICc	Δ AICc	w_i
Prey density and relative abundance						
11	*deer_p_avail*[a] *elk_p_avail*[b] *moose_p_avail*[c]	-24.68	3	56.16	10.16	0.00
17	*deer_d*[d] *elk_d*[e] *moose_d*[f]	-25.95	3	58.70	12.69	0.00
Environmental characteristics						
9	*ter_rug*[g]	-26.48	1	55.08	9.08	0.00
18	*all_linear*[h] *edge*[i] *open*[j]	-26.12	3	59.04	13.04	0.00
Physical characteristics						
2	*age*[k] *sex*[l] *cougkg*[m]	-20.59	3	47.98	1.98	0.14
16	*cougkg*	-27.77	1	57.67	11.66	0.00
Physical & Environmental						
5	*ter_rug age sex cougkg*	-19.86	4	49.11	3.10	0.08
7	*age sex cougkg all_linear edge open*	-17.52	6	50.16	4.16	0.05
8	*age sex edge*	-22.89	3	52.58	6.57	0.01
13	*cougkg edge*	-26.00	2	56.39	10.39	0.00
15	*age sex kittenage all_linear edge open*	-20.82	6	56.75	10.75	0.00
19	*cougkg all_linear edge open*	-25.16	4	59.69	13.69	0.00
Comprehensive						
1	*age sex cougkg deer_p_avail*	-18.31	4	46.00	0.00	0.38
3	*age sex cougkg deer_p_avail elk_p_avail moose_p_avail*	-16.46	6	48.02	2.02	0.14
4	*age sex cougkg ter_rug open deer_p_avail*	-16.70	6	48.51	2.51	0.11
6	*age sex cougkg edge deer_p_avail elk_p_avail moose_p_avail*	-15.56	7	49.42	3.41	0.07
10	*cougkg edge deer_p_avail*	-24.24	3	55.27	9.27	0.00
12	*cougkg ter_rug open deer_p_avail*	-23.40	4	56.19	10.18	0.00

14	*cougkg ter_rug deer_p_avail elk_p_avail moose_p_avail*	-22.24	5	56.62	10.62	0.00

[a] Relative abundance of deer
[b] Relative abundance of elk
[c] Relative abundance of moose
[d] Density of deer
[e] Density of elk
[f] Density of moose
[g] Average terrain ruggedness calculated using a 500m moving window
[h] Kilometers per km^2 of linear features (seismic lines, pipelines, and roads)
[i] Proportion of edge habitat (100m buffer around intersection of forest and open habitat)
[j] Proportion of open habitat
[k] Cougar age (A = 1, SA = 0)
[l] Cougar sex (M = 1, F = 0)
[m] Cougar mass (kg) including mass of dependent kittens

The top fractional multinomial model fit the cougar preference data well ($R^2 = 0.71$). The probability of cougars killing larger prey (elk, moose, and feral horses) increased if the cougar was an adult and if it was male (Table 5.7). The responses to relative abundance of deer and cougar mass are more difficult to interpret. Where cougars killed moose and horses in winter, for instance, the strength of selection apparently increased as the relative abundance of deer increased, but any effect of prey switching might be captured in the strongly negative constant term for moose and horses, which were always less abundant than deer. Selection for elk, on the other hand, showed a negative relationship with the relative abundance of deer (Table 5.7), a pattern consistent with prey switching. Cougars with the highest biomass (i.e., females with large kittens) were less likely to kill elk or moose and more likely to focus on deer. But for feral horses, which were killed only by male cougars during winter, preference increased with cougar body size.

Table 5.7: Coefficients, standard errors, *P* values and 95% confidence intervals for the highest ranked fractional multinomial regression model used to predict cougar preference (P_j) for deer, elk, moose, and feral horses in west-central Alberta in winter during 2005–2008. Deer are the reference category to which other coefficients are compared.

Species	**Variable**	**Coefficient**	**Standard Error**	***P***	**95% Confidence Interval**
Elk	*age*[a]	0.725	1.099	0.510	-1.429, 2.879
	sex[b]	0.882	0.938	0.347	-0.957, 2.721
	cougkg[c]	-0.020	0.016	0.203	-0.051, 0.011
	deer_p_avail[d]	-6.465	5.120	0.207	-16.499, 3.569
	Constant	3.402	4.359	0.435	-5.141, 11.944
Moose	*age*	20.50	1.657	0.000	17.258, 23.757
	sex	7.065	3.424	0.039	0.354, 13.776
	cougkg	-0.179	0.066	0.007	-0.0309, -0.049
	deer_p_avail	9.196	11.1092	0.408	-12.577, 30.969
	Constant	-21.728	7.420	0.003	-36.273, -7.185
Feral horse	*age*	41.278	1.700	0.000	37.946, 44.611
	sex	71.350	3.170	0.000	65.136, 77.563
	cougkg	0.331	0.021	0.000	0.288, 0.373
	deer_p_avail	376.025	21.187	0.000	334.498, 417.553
	Constant	-374.541	19.163	0.000	-412.101, -336.983

[a] Cougar age (A = 1, SA = 0)
[b] Cougar sex (M = 1, F = 0)
[c] Cougar mass (kg) including mass of dependent kittens
[d] Relative abundance of deer

Evaluating the MSFR

Fitting equation 5.7 for each cougar (i) using the fixed value for A (10km^2/day), and empirically estimated values for C_i (kg/day), P_{ij} (Manly’s preference for each prey for each cougar), M_{ij} (average size for each prey species for each cougar), and N_{ij} (density of each prey in the home range of each cougar) predicted species specific kill rates perfectly (linear regression where intercept = 0, slope = 1, and $R^2 = 1$). Thus, the MSFR I propose is structurally sound and capable of accurate prediction. When I incorporated values predicted using the top models for C and P_i into equation 5.7 and maintained A at the fixed value of 10km^2/day, assigned mean winter values for M_j, and used observed N_{ij}, I found that the complete MSFR produced a good fit ($R^2 = 0.82$) to the prey specific kill rate data for individual cougars (Figure 5.4). However, the model over-predicted predation for deer and under-predicted for less abundant species (Table 5.8).

Table 5.7: The difference between the total number of deer, elk, moose and feral horses killed by 34 cougars during a 180 day winter as estimated using empirical kill rate data and kill rates generated using a multi-species functional response (MSFR, Equation 5.7). Parameter values were obtained as follows: A was fixed at 10km^2/day, C_i and P_{ij} were estimated using the top models for each (Tables 5.4 and 5.6, respectively), M_{ij} were the average weights of each prey type killed by cougars in winter (deer = 60kg, elk =194kg, moose = 288kg, feral horse = 362kg), and N_{ij} was the empirically estimated density of each prey in the home range of each cougar.

Species	Empirically estimated	MSFR generated	Difference
Deer	516	591	+15%
Elk	29	25	-14%
Moose	14	13	-7%
Feral horse	18	11	-39%

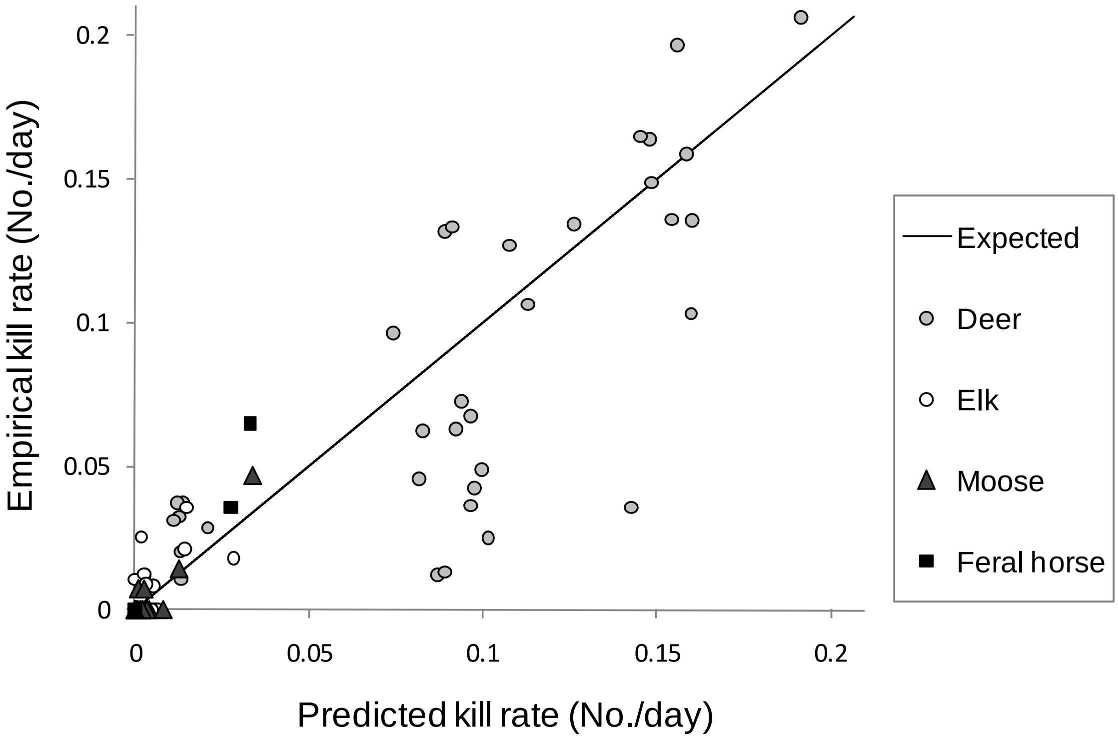

Figure 5.4: Fit between empirically estimated kill rates and kill rates estimated using equation 5.7 for 4 prey types (deer, elk, moose, and feral horses) for each of 34 cougars monitored in west-central Alberta during winter 2005-2008. Parameter values were obtained as follows: A was fixed at 10km^2/day, C_i and P_{ij} were estimated using the top models for each (Tables 5.4 and 5.6, respectively), M_{ij} were the average weights of each prey type killed by cougars in winter (deer = 60kg, elk =194kg, moose = 288kg, feral horse = 362kg), and N_{ij} was the empirically estimated density of each prey in the home range of each cougar.

DISCUSSION

I developed a mechanistic MSFR model capable of simultaneously predicting the rate at which a predator kills each of several prey types and fit it to data from cougars foraging in a diverse multi-ungulate system in west-central Alberta. Structurally, the model was based on Holling's disc equation, but also incorporated Manly's preference terms for each prey (Joly and Patterson 2003) to accommodate variation in selection due, for example, to differential vulnerability or prey switching. I attempted to integrate additional realism by allowing parameter values to vary as a function of a series of covariates, permitting kill rate to respond to more than just prey density (Nilsen et al. 2009, Webb 2009). My parameterized model fit the data remarkably well, suggesting that my approach might offer useful insight into the effects cougars have on prey in multi-prey systems. Cougar MSFR can be considered in 2 interrelated parts: 1) aggregate kill rate, which defines the overall magnitude of cougar predation and is a function of aggregate prey density, the efficiency parameter, and consumption rate, and 2) decomposition of aggregate kill rate into species-specific kill rates, which is influenced by relative abundance and preference (encompassing differential vulnerability, prey switching, and individual specialization). I address each in turn before focusing on implications for managing cougar predation on small populations of ungulate prey in multi-prey systems.

Aggregate Kill Rate

Little of the substantial variation I observed in cougar aggregate kill rate could be explained by variation in prey density, a result consistent with the findings of most other studies of large carnivore functional response (Dale et al. 1994, Hayes et al. 2000, Eberhardt et al. 2003, Jost et al. 2005, Nilsen et al. 2009). Hence, strictly prey-dependent functional response models are probably not useful for investigating the effects large carnivores have on prey. Instead, my results reinforce recent studies demonstrating that determinants of kill rate other than prey density must be considered to improve the fit and utility of large carnivore functional response models (Vucetich et al. 2002, Jost et al. 2005, Nilsen et al. 2009, Webb 2009). Nevertheless, kill rate must go to 0 when prey go to 0, and so using a prey-dependent model to provide the basic structure underpinning aggregate kill rate remains biologically reasonable.

Ostensibly, variation in prey density does not explain much of the variation in large carnivore kill rate because of satiation, which occurs when additional prey no longer confer an advantage in terms of the predator's ability to locate and subdue its next meal. Studies of wolves (Dale et al. 1994, Hayes et al. 2000, Eberhardt et al. 2003) and European lynx (*Lynx lynx*; Nilsen et al. 2009) suggest that large carnivores reach satiation at very low prey density. Although my data indicates that cougars also reach satiation quickly, I was unable to ascertain the precise shape of the functional response to low aggregate prey density, or identify the factors that might cause this to vary. Establishing the point on the prey axis below which cougar aggregate kill rate begins to decline as a function of prey density is an important task for future research.

Efficient predators have a greater capacity to limit small populations of alternate prey because low prey density does not prevent high kill rate (Sinclair et al. 1998). Whether or not small populations persist will depend on prey selection (see next section) and the factors causing kill rate at satiation to vary. Cougars were satiated well below the limit set by physical handling time. Because cougars risk injury or death when they prey on ungulates (Ross et al. 1995, Logan and Sweanor 2001, Murphy and Ruth 2009) and must expend energy locating and capturing prey, kill rate at satiation might be a result of tradeoffs between the costs and benefits of predation (Abrams 1982, 1990). Indeed, most carnivores may stop killing once their basic energetic requirements are met, leaving them with extra time for other activities (Jeschke 2007). That cougars have 'spare time' between handling events is evident in the ability of female cougars to increase kill rate simply by increasing hunting effort when they have kittens (Table 5.3). A cost-benefit approach to satiation, moreover, explains surplus predation on easily killed domestic stock (Mazzolli et al. 2002), increased kill rates in summer when juvenile ungulates pose little risk to cougars (Chapter 4), and higher kill rates by more effective mature cougars (Chapter 4).

In the MSFR defined by equation 5.7, aggregate kill rate for a satiated predator is determined by consumption rate (kg of prey/unit time) and the size of prey killed. For cougars in west-central Alberta during winter, the most important drivers of consumption rate were the age, sex and metabolic requirements of individuals, accounting for just over half of the observed variation. This makes sense in light of a cost-benefit view of satiation as these are the very factors that might be expected to change this relationship. This result also underscores the importance of cougar population structure for determining maximum number of ungulates removed (Chapter 4). Surprisingly, habitat variables did not influence aggregate kill rate. Cougars are thought to prefer edge habitat and to have poor hunting success in open habitats (Laundré and Hernández 2003, Holmes and Laundré 2006). Increased availability of effective hunting habitat might therefore facilitate predation. None of the habitat covariates I used were important in the consumption rate model, however, possibly because cougar home ranges in west central Alberta always were above necessary hunting habitat thresholds (e.g., a functional responses in habitat selection; Mysterud and Ims 1998).

Recent work on wolves convincingly demonstrates that predator interference can have a considerable impact on large carnivore kill rate (Vucetich et al. 2002, Jost et al. 2005, Becker 2008), a finding that is largely responsible for increased prevalence of ratio-dependent models in the large carnivore literature (Garrott et al. 2007). Unfortunately, I did not have sufficient data on cougar density at the home-range scale to test the influence of predator interference on cougar MSFR, but its potential importance is highlighted by the negative relationship I observed between kill rate (Y_t) and prey density after controlling for cougar sex, age, metabolic demands, and average prey size (Table 5.2). Cougars have been shown to congregate in places where prey are abundant (Pierce et al. 2000), potentially leading to increased competition at higher prey density and explaining the unexpected decline in kill rate as prey density increased. Despite my inability to assess predator interference, the MSFR model structure I present can accommodate interference by incorporating predator-prey ratios as covariates influencing efficiency, satiation, or both, thereby injecting ratio-dependence into the functional response without any of the structural problems associated with traditional ratio-dependent models (Abrams 1990, Appendix VI).

Species-Specific Kill Rate

Species-specific kill rate depended on the relative availability of various prey types and on cougar preference for each. Cougars in west-central Alberta were selective predators, rarely killing prey in proportion to availability, meaning that preference played a large role in determining prey composition. The most important explanatory variables for preference during winter remained cougar age, sex, and size. These variables were in each model carrying an AIC weight > 0.01 and alone comprised the second-ranked model, less than 2 AIC units behind the top model, which incorporated an additional term for deer relative abundance. As in the case of consumption rates, habitat variables were conspicuously absent from top ranked preference models. Younger cougars and females tended to select smaller prey (deer or sheep), but mature cougars, especially adult males, were less likely to avoid larger prey types (moose, elk, and feral horses), occasionally selecting strongly for them. Thus, just as for aggregate kill rate, cougar population structure played a defining role in the number of each prey type killed.

Prey Switching

Whereas prey density was unimportant for establishing aggregate kill rate across the range of ungulate densities available in west-central Alberta, the relative abundance of different species had a substantial influence on prey composition. Importantly, preference increased with relative abundance, consistent with Murdoch's (1969) definition of prey switching. Although I was unable to rule out density independent preference for deer by cougars (because deer were always the most abundant prey), switching appears to be a more parsimonious explanation. My reasons for this assertion are 1) selection tended to increase with increasing relative abundance when each prey type was considered independently, and 2) cougars inhabiting systems not dominated by deer often select for other, more abundant prey types (e.g., elk; Hornocker 1970, Murphy 1998, Nowak 1999).

As expected for a switching predator, the top fractional multinomial model for cougar preference included a term for the relative abundance of deer, but the coefficients associated with this term did not always match the expected switching values (i.e., the relationship between preference and deer abundance was positive for moose and feral horses). Because deer were always the most abundant prey, however, much of the variation in preference due to prey switching appears to have been captured in the constant terms for each species in the model. Thus, incorporating the estimated fractional multinomial preference function into a cougar MSFR might fail to adequately characterize switching, resulting in poor prediction where relative abundances of prey are very different from those observed during my study. Adequate parameterization of the preference function and a better assessment of the importance of prey switching in cougar MSFR will require research in systems where the relative abundance of prey is more variable across individual home ranges than it was in west-central Alberta.

In any case, the tendency for cougars to avoid the least abundant prey during my study (e.g., bighorn sheep, feral horses) suggests that these populations may have reduced exposure to the risks posed by asymmetrical apparent competition (DeCesare et al. 2009). The security switching affords small populations of less abundant prey, however, is unlike the security expected under a Type III functional response, although the existence of the former is often used to justify the application of the latter (Varley and Boyce 2006). The key difference is that predators following a Type III functional response kill few prey at low *density* while switching predators avoid prey at low *relative abundance*. Thus, for switching predators, if the relative abundance of a small population increases, it can be subject to increasing predation rates, even as its density declines.

In New Mexico, for instance, bighorn sheep coexisted with cougars and mule deer until the mule deer population declined in response to a severe drought, after which cougar predation rapidly drove the bighorn population to extinction (Logan and Sweanor 2001). Consequently, equation 5.7 may provide a more realistic approach to modeling prey switching than traditional Type III equations because it allows for the stability created by switching when alternate prey are abundant, but does not impose a refuge at low density when primary prey become scarce and efficient predators turn their attention to alternate food sources.

Individual Specialization

In addition to providing the first quantitative assessment of prey switching in cougars, I also provide the first evaluation of the prevalence of individual specialization in a cougar population. Although individual cougars often killed several types of ungulate prey, SSI_i indicated that most individuals specialized, focusing on a single prey type for which they selected strongly. On the other hand, PS_i and W_i indicated generalist predation. This contrast occurred because cougar prey specialization was fundamental as opposed to realized (Bolnick et al. 2003). Because most cougars specialized on deer (Table 5.1), PS_i and W_i scores for individuals feeding on this species were high, misleadingly suggesting generalist predation. Consequently, SSI_i may be the most appropriate index for assessing specialization where it is fundamental in nature. In addition to deer, cougars specialized on the majority of other available ungulate prey types including elk, bighorn sheep, moose, and feral horses. Because deer were always the most abundant prey, specialization on this species also was consistent with prey switching.

The parameterized MSFR I fit for cougars overemphasized the importance of cougar preference for deer and underemphasized it for less abundant prey (elk, moose, and feral horses). Despite excellent overall fit, therefore, the model may misjudge risk to small populations of endangered prey. The source of most of the risk to these populations came from those cougars that did not conform to the typical switching pattern, specializing on prey that occurred at low relative abundance. The fate of small populations of alternate ungulate prey exposed to cougar predation, therefore, may be a direct result of the establishment of one or more specialists (Festa-Bianchet et al. 2006), and not necessarily to the simple presence of a healthy cougar population.

For example, a small and isolated population of bighorn sheep near the center of my study area at Ram Mountain declined from over 220 individuals in the early 1990's to fewer than 45 in 2002. Initially, the decline was a result of density dependent factors (Portier et al. 1998), but subsequent cougar predation forced the population to very low levels (Festa-Bianchet et al. 2006). Cougar predation on bighorns ceased abruptly in 2003, a phenomenon Festa-Bianchet et al. (2006) attribute to the death or emigration of an individual specialist, although no data on cougars were available to support this hypothesis. During 2005-2008 I monitored 9 cougars with ranges overlapping the Ram Mountain bighorn sheep population, locating 313 predation events of which only one was a bighorn sheep. Despite a cougar density of 2.71-3.49/100 km^2 estimated in the vicinity of Ram Mountain during this period (Appendix 1), the number of resident ewes increased by 23% (from 17-21; M. Festa-Bianchet, personal communication).

Cougar specialization was fundamental, not realized (Bolnick et al. 2003) and cougars apparently developed a strong search image for their prey of choice. For example, I monitored a sub-adult female who specialized in bighorn sheep, moving from one alpine slope to another and ignoring abundant deer in the valleys in between. The predictable location of some ungulates, especially during winter, probably facilitates efficient predation on less abundant prey. Although specialist predation on small populations of ungulates has been modeled as a stochastic process (Festa-Bianchet et al. 2006), determining the mechanisms underlying search image development might make specialization more predictable, greatly facilitating management. Specialization travels along matralines in some mammals (Estes et al. 2003), but although cougars spend up to 20 months with their mothers, this cannot be the sole explanation for search image development since females never specialized in larger prey while males did so frequently. Obviously, this trait was not passed from mother to son.

Another hypothesis is that specialization arises from an ideal free distribution (Fretwell and Lucas 1970, Estes et al. 2003). The ideal free distribution predicts that some individuals in a population of specialists will be better off focusing on prey items of intrinsically lower value (e.g., higher risk or more difficult to find) when the realized benefit of intrinsically higher value prey is reduced by intraspecific competition. Because of their larger size, adult males can exploit larger prey with less risk than other cougars (Sunquist and Sunquist 1989) making this their optimal strategy where smaller ungulates are heavily exploited by conspecifics. Importantly, specialization on less abundant prey should be density dependent under an ideal free distribution (Estes et al. 2003), meaning that negative effects on small populations of alternate prey will be less likely where there are fewer cougars. This compelling hypothesis requires further testing.

Managing Cougar Predation on Small Populations of Alternate Prey

A management solution commonly advocated for problems of apparent competition is to reduce primary prey, with or without concurrent predator reductions (Courchamp et al. 2003). Whether or not the predator involved exhibits prey switching clearly has important implications for the efficacy of this strategy. Courchamp et al. (2003) used a simple model where predators consumed prey in proportion to availability and showed how removing feral pigs (*Sus scrofa*) to reduce golden eagle (*Aquila chrysaetos*) predation on endangered island foxes (*Urocyon littoralis*) might actually increase predation in the short-term before eagles could be removed because the relative abundance of foxes was higher. The difference between predation rates prior to and then after removal of primary prey would be even more dramatic for a switching predator. Consequently, where primary prey removals are planned to protect endangered populations of ungulate prey from predation by cougars, success will depend on removing cougars also, which will be most effective if enacted prior to primary prey reductions (Collins et al. 2009) and must be of sufficient magnitude to account for any increased preference that accompanies increased relative abundance of the at-risk prey.

Large-scale reductions in predators and/or primary prey to reduce the effects of apparent competition on small populations of alternate prey can be politically unsavory however (Courchamp et al. 2003), and the utility of such extreme measures is often questioned (Weclaw and Hudson 2004). Thus, where cougar predation negatively affects small populations of alternate prey through individual specialists, the least intensive management solution might be to target those individuals. However, identifying specialists and targeting them for removal presents an important challenge because collaring or other intensive monitoring strategies are not always available (Knopff and Boyce 2007). Moreover, maintaining cougar populations below carrying capacity (e.g., through sport hunting) might reduce predation on small populations of ungulate prey if specialization is density dependent and results from individuals diverging from a standard switching pattern because the realized benefits of focusing on the most abundant prey are diminished by intra-specific competition.

Summary

Cougar MSFR in west-central Alberta was driven primarily by cougar population structure and relative abundance of alternate prey, not by prey density. As a result, cougar predation is more likely to limit ungulate populations than it is to regulate them. Regulatory predation is inherently stabilizing, whereas limiting predation is not (Messier

1991). Hence, limiting predation is a greater concern where conservation of endangered prey is at stake. The nature and importance of predation as a limiting factor for each ungulate population in a multi-prey system will be driven substantially by cougar population structure. A tendency toward prey switching by cougars, however, means that small populations of alternate prey that also have very low relative abundance may generally be protected from cougar predation. This is consistent with frequent persistence of small populations of alternate ungulate prey, even where healthy cougar populations are present. Exceptions come from individual cougars that specialize on small populations of prey, and these individuals pose the primary risk to such populations. My results therefore support the idea that the dynamics of small populations of ungulate prey subject to cougar predation may be substantially affected by the rise and fall of individual specialists (Festa-Bianchet et al. 2006).

More research into cougar MSFR is clearly required. For instance, the importance of prey switching for cougars will be better assessed where relative abundance of prey is more variable at the home range scale than it was in west-central Alberta. Moreover, it will be especially important to determine what drives patterns of specialization. Whether specialization follows an ideal free distribution in a density dependent fashion or is idiosyncratic has significant implications for managing the effects of cougar-mediated apparent competition for small populations of alternate prey.

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CHAPTER 6

ARE COUGARS NOCTURNAL AMBUSH PREDATORS?

Behavioral strategies employed by predators can play a crucial role in the ecology of predator-prey systems. For example, whether predators use ambush (sit and wait) or active (mobile search and pursuit) hunting strategies influences prey behavior (Schmitz and Suttle 2001), the stability of predator-prey systems (McCauley et al. 1993, Wilmers et al. 2007), and community structure and biodiversity (Schmitz 2008). Similarly, diel and seasonal modifications in hunting effort causes predation risk to vary over time, which also has substantial ramifications for prey behavior and population dynamics (Fenn and MacDonald 1995, McIntosh and Townsend 1996, Lima and Bednekoff 1999, Mitchell and Lima 2002). Indeed, temporal variation in predation risk is a fundamental component of the complex games of stealth and fear that can structure entire communities (Brown et al. 1999, Kotler et al. 2002).

In large mammal systems, these behaviorally driven phenomena also have ramifications for conservation and management. Ambush predators are believed to be less selective than their active counterparts, for instance, killing prey items as they come into range of a surprise attack without focusing on young, sick, or senescent animals as do active predators (Husseman et al. 2003, Wilmers et al. 2007). This results in a higher additive component of predation for ambush predators, which can produce tighter regulation of prey populations and might increase the stability of large mammal communities in the face of climate change (Wilmers et al. 2007). Higher additive predation also is more likely to maintain prey at low equilibrium longer (Wilmers et al. 2007), an important distinction for wildlife managers attempting to increase ungulate populations in the face of predation. Where large carnivores pose a risk to humans and livestock, moreover, understanding temporal variation in hunting behavior is essential for managing conflict and advancing conservation (Woodroffe 2000, Patterson et al. 2004, Sweanor et al. 2008). Human-carnivore conflict can be reduced where predators exhibit consistent hunting patterns over a diel period, but this becomes more challenging if predation is temporally stochastic (Ogada et al. 2003, Sweanor et al. 2008).

Despite theoretical and practical motivation for defining the hunting strategies of large carnivores, rigorous quantitative assessments are rare. Cougars (*Puma concolor*), for instance, influence ungulate population dynamics and ecosystem structure (Wehausen 1996, Logan and Sweanor 2001, Ripple and Beschta 2006, 2008), commonly kill livestock and pets in some places (Cunningham et al. 1999), and occasionally attack people (Beier 1991, Baron 2004, Torres 2005). Yet, cougar hunting strategies remain only superficially understood. Cougars are variously described as ambush (sit-and-wait) and active (stalking) predators (Kunkel et al. 1999, Pierce et al. 2000, Rominger et al. 2004, Krumm et al. 2009), and although ambush predation has been assumed when modeling the effects of cougars on prey (Wilmers et al. 2007) it is not clear which strategy dominates. Similarly, while cougars are normally considered nocturnal and crepuscular hunters (Beier et al. 1995, Anderson and Lindzey 2003, Sweanor et al. 2008), the degree to which they are physiologically constrained to hunting at night or are capable of diurnal hunting but simply mimic nocturnal activity of primary prey (e.g., Beier et al. 1995) is unknown. Moreover, although understanding the predictability of predation risk at broad temporal scales (e.g., nocturnal vs. diurnal) clearly has significant ramifications for predator-prey dynamics and human safety (Fenn and MacDonald 1995, McIntosh and Townsend 1996, Sweanor et al. 2008), variation at finer scales also is important (Roth and Lima 2007, Ferrari and Chivers 2009), but has not yet been evaluated for cougars.

Modern global positioning system (GPS) telemetry provides an efficient means to fill these knowledge gaps. Precise spatial locations generated automatically at regular intervals throughout the day can provide information on temporal variation in large carnivore activity patterns. In addition, recently developed GPS telemetry applications for identifying predation events (e.g., Anderson and Lindzey 2003, Chapter 2) offer a means to link movement and predation, providing new opportunities to evaluate behavioral strategies used by hunting mammals.

For this chapter, I employed data on diel and seasonal variation in cougar activity and predation patterns derived from GPS telemetry to assess cougar hunting behavior. First, I linked movement rates to the timing of predation events to investigate whether cougars primarily employ an active or ambush strategy. Next, I attempted to determine whether the timing of cougar predation was inherently predictable or stochastic. To do so, I tested whether cougars exhibited temporal peaks and troughs in diel hunting behavior (i.e., nocturnal predation), and used temporal autocorrelation analysis to quantify the strength of the pattern. Finally, I used movement patterns derived from elk (*Cervus elaphus*) GPS data to test the hypothesis that predictability in predation is driven by the activity levels of prey (Curio 1976, Beier et al. 1995, Karanth and Sunquist 2000). I discuss the implications of my results for cougar interactions with prey and reducing human-cougar conflict.

METHODS

I studied cougar hunting behavior in west-central Alberta, Canada, during 2005-2008. My study area was centered approximately at 52°18'N, 115°48'W and encompassed 16,900-km^2 of mountains and foothills in Clearwater County, bordering Banff and Jasper National Parks. The primary prey of cougars in the region were white-tailed deer (*Odocoileus virginianus*), followed by mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and elk (*Cervus elaphus*), although a diversity of prey were incorporated into cougar diets (Chapter 4). Additional details of the topography, climate, flora and fauna of this region can be found in Chapters 2-4.

I used data from 41 cougars captured and radiocollared during December 2005–May 2008. Capture was accomplished by pursuing and treeing cougars using hounds, then chemically immobilizing them using intramuscular remote drug delivery (Pneu-Dart Inc., Williamsport, Pennsylvania, USA) at an intended dose of 3 mg/kg zolazepam-tiletamine (Telazol®, Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and 2 mg/kg xylazine (Rompun®, Bayer, Inc., Toronto, Ontario, Canada). After immobilizing each cougar, I instrumented it with a Lotek 4400S GPS collar (Lotek Engineering, Newmarket, Ontario, Canada) programmed to collect eight location fixes per day at three hour intervals (00:00, 03:00, 06:00, 09:00, 12:00, 15:00, 18:00 21:00). All animal handling procedures followed the guidelines of the American Society of Mammalogists (Gannon and Sikes 2007), and captures were conducted under the authority of the Province of Alberta Collection and Research Permit 19872 CN, and were approved by the University of Alberta Animal Care and Use Committee for Biosciences (Protocol # 479505).

I identified predation events by visiting clusters of ≥ 2 GPS locations occurring within 200m of each other and within 6 days using a space-time algorithm (Chapter 2). I visited nearly all GPS location clusters during December 2005–October 2007 and employed a logistic regression model (Chapter 2) to screen clusters with a near-zero probability of predation from the set I visited during November 2007–August 2008. This method allowed me to locate most prey >8 kg killed by cougars over the duration that each animal was monitored (Chapters 2 and 4). Following Anderson and Lindzey (2003) and Matson et al. (2007), I assumed the time of the first location at a predation cluster indicated the kill was made during the preceding 3-hour interval. I only used data from predation clusters where the GPS location prior to the first fix at the cluster also was obtained and the timing of the arrival of the cougar at the cluster could be accurately assigned to a specific 3-hour interval. I used winter snowtracking data to test the assumption that cougars do not wait in ambush for >3 hours at a time.

I was primarily interested in cougar behavior while hunting and not while handling prey at kill sites (i.e., when the lack of movement could be attributed to the presence of a carcass). I therefore divided cougar GPS locations into those associated with handling prey and those associated with searching for it. All locations obtained at clusters where a predation or scavenging event was identified were assigned to the handling category, while all other locations were considered searching (Chapter 4). Diel variation in cougar activity levels while hunting was assessed by calculating the straight-line distance between consecutive 3-hour GPS locations (i.e., step length) ending in a search location and comparing the average distance moved among the 8 time periods conforming to the fix schedule of the collars. Steps spanning more than one 3-hr interval due to poor fix success (i.e., where GPS location data were not obtained) were excluded from all analyses. I analyzed predation and movement data separately for winter (October 15-April 14) and summer (April 15-October 14), because these seasons encompassed many of the broad shifts in temperature, daylight, snow accumulation, and prey availability, vulnerability, and behavior that can influence large carnivore predation (Chapter 4).

Some ecologists use movement behavior to quantify foraging strategy, assuming that active predators move more often and over longer durations than ambush predators (e.g., Perry 1999). This approach is inadequate, however, because animals can move or remain still for reasons unassociated with predation. A true test of foraging strategy must evaluate whether predators capture more prey during periods of time when they are moving (active predation) or when they remain still (ambush predation). I therefore linked movement rates and predatory success in each diel interval in each season to identify the primary hunting strategy employed by cougars. I predicted that the average movement during 3-hour intervals should be unrelated or negatively correlated with the frequency of predation during each interval if cougars employ a sit-and-wait strategy. Conversely, I predicted that if cougars are active predators, frequency of predation would be positively correlated with movement during 3-hour intervals. I evaluated these predictions using a Pearson's correlation between the average distance moved and the proportion of predation events made by cougars during each 3-hour diel interval in each season.

To assess within-season predictability in activity and predation patterns in relation to daylight, I divided predation events into four time blocks in each season; i.e., those made 1) in the early morning (incorporating dawn), 2) during the day, 3) in the evening (incorporating dusk), and 4) overnight. Sunrise occurred between 5:43–8:42 in winter and 4:13–7:00 in summer and sunset took place between 17:05–19:30 in winter and 18:15–21:01 in summer (http://www.nrc-cnrc.gc.ca/eng/services/hia/sunrise-sunset.html). Thus, in both seasons kills occurring between 3:00 and 9:00 were assigned to morning, while kills assigned to the evening period occurred between 15:00 and 21:00 in winter and 18:00 and 24:00 in summer. During winter, therefore, each diel division consisted of 2 GPS fix intervals, while in summer the diurnal period consisted of three intervals and the nocturnal period consisted of only one. I used contingency table analysis to test the null hypothesis that cougars made kills uniformly (i.e., randomly) throughout the day in each season. Expected frequencies were calculated assuming an equal distribution of kills in each period, adjusted for the length of the period.

I also used a contingency table to assess seasonal variation in the relative frequency of killing during each of the 4 primary diel divisions (i.e., morning, day, evening, night). I controlled for the seasonal shift in the total amount of time available for cougars to make kills in each category by dividing the frequency of kills in each cell in summer by the number of GPS time intervals used to obtain the count. This reduces total sample size of the contingency table analysis, effectively making the test more conservative by reducing the chi-square value (Zar 1999).

I used autocorrelation functions (ACFs) to evaluate temporal predictability in cougar movement behavior at the temporal resolution of the 3-hour interval in each season. Autocorrelation functions can be usefully applied to assess consistency in periodic patterns of animal behavior (Boyce et al. 2010). To produce an ACF for cougar step-length while hunting (i.e., search locations), I developed a time series by assigning a unique sequential number to each 3-hour fix attempt (whether successful or not) for each cougar. Autocorrelation values were calculated out to 30 lags (90 hours), and the number sequences for different cougars were separated by >30 units so that autocorrelation values were calculated only within the time series of an individual cougar but applied at the population level. Autocorrelation analysis was performed using the corrgram command in STATA 10.0 (StataCorp, College Station, Texas, USA), which filters gaps created by missed fixes (including the removal of all fixes created during handling events) and averages autocorrelation values at each time lag across all individual cougars. I analyzed the data for summer and winter separately to investigate potential seasonal differences in the pattern or magnitude of ACFs.

To test the hypothesis that cougar activity levels mirror those of their prey, I compared cougar movement data to that collected from 18 resident female elk obtained during 2000-2003 in the same study area where cougar data were collected. Elk were captured using a netgun fired from a helicopter (Province of Alberta collection and research permit 1432GP and University of Alberta protocol # 300401) and fitted with a Lotek GPS 2200 collar programmed to obtain a location fix every 2 hours (0:00, 02:00, 04:00, … , 18:00, 20:00, 22:00). Additional details regarding elk capture and monitoring can be found in Frair (2005). I used GPS relocation data and assigned elk movements to each 2-hour diel interval, in each season, using techniques identical to those described above for cougars. Because the GPS intervals were different for elk and cougars (i.e., 2hrs vs. 3hrs), direct statistical comparisons in diel movement rates for predator and prey required that the data for one of the species were adjusted. I adjusted elk movement data to match the 3-hour interval of cougars by splitting every second 2-hr interval and assigning half the movement each to the preceding and following intervals. I then evaluated cougar response to elk movement using a Pearson's correlation. If cougar activity patterns are driven by those of their prey, I expected a strong, positive relationship between elk and cougar movement rates. In addition to statistical comparisons using adjusted data, I plotted raw elk movement data (i.e., at 2hr intervals) in each season to permit visual comparison in activity patterns between species.

RESULTS

I monitored the movements and predatory behavior of 41 cougars collared with Lotek 4400S GPS collars over 8,976 cougar days. Monitoring predation sequences (Figure 6.1) yielded 45,874 GPS locations and 1,254 predation events. The fix success of individual collars deployed on cougars during this study was low, averaging 67% (SD = 16%), constraining my ability to accurately assign distance traveled or the first fix at predation clusters to specific 3-hour intervals. Only 72% (n = 19,533) of cougar searching locations, and only 50% of the first locations at cougar predation clusters (n = 630) were preceded by a successful fix 3 hours earlier. All data failing to meet these criteria were excluded from analysis. I conducted >400km of snowtracking and located 41 predation events using this technique. Although cougars occasionally crouched or paused during stalking sequences, they did not wait in ambush for extended periods (i.e., in beds) immediately prior to making a kill. This validates my assumption that the first fix at a predation cluster indicated that the kill was made during the preceding 3-hour interval, provided that the fix at the beginning of the preceding interval also was successfully obtained.

On average, the straight line distance between 3hr fixes generated by hunting cougars was 917 m (SD = 214) in summer and 772 m (SD = 216) in winter. Variation in diel movement patterns was evident between seasons and cougars exhibited peaks in movement during the morning and evening in summer, with a pronounced lull in activity during the day. In winter, on the other hand, movement was lowest just before dawn and rose steadily throughout the day, peaking in the evening before declining overnight (Figure 6.2). Movement and predation incidents within 3-hour intervals were strongly and positively correlated in both seasons (summer: $R = 0.76$, $P = 0.028$; winter: $R = 0.93$,

$P < 0.001$; Figure 6.2), indicating that cougar hunting success was related to the effort invested in actively searching for prey. Moreover, cougar movements during 3-hour intervals where predation occurred averaged 1,055 m in summer (SD = 845) and 1,081 m (SD = 887) in winter (data are strongly skewed to the right; Figure 6.3), representing a 40% increase over the average 3-hour search movement in winter and 15% in summer, despite the fact that movement during intervals where predation occurred was truncated by the predation event. Paired data for individual cougars indicate this difference was significant in winter ($t_{37} = -2.80$, $P = 0.008$), but not summer ($t_{29} = -1.77$, $P = 0.086$). Collectively, these data consistently point to active predation by cougars.

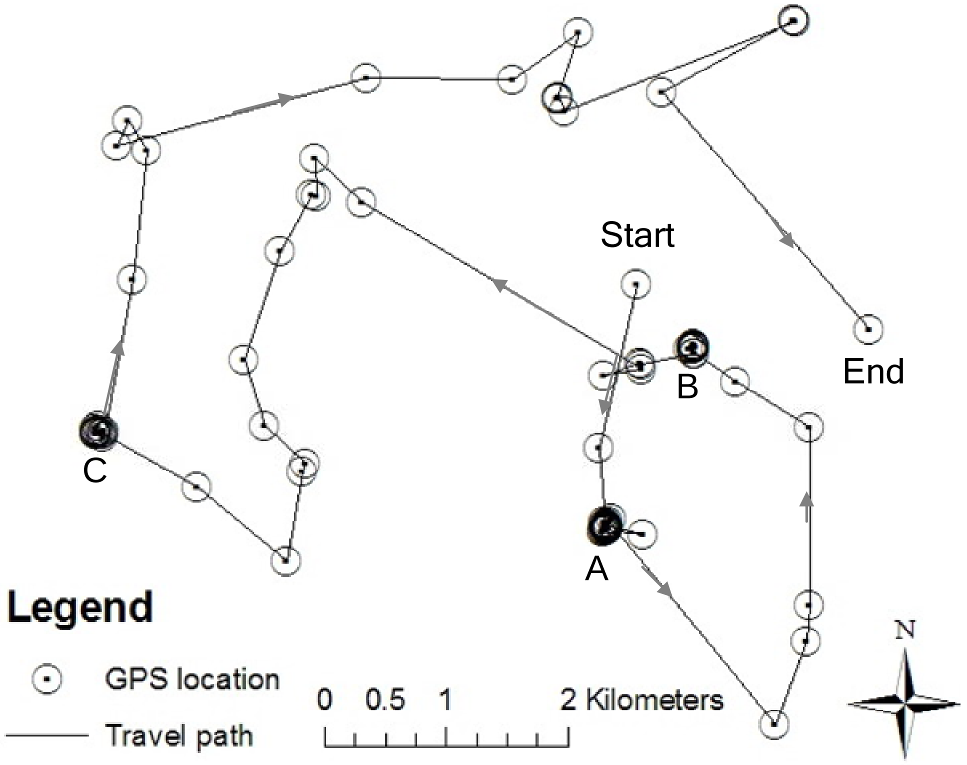

Figure 6.1: A truncated predation sequence demonstrating the typical movement behavior of a cougar in west-central, Alberta, Canada during 2005-2008. The sequence displayed is derived by drawing a straight line between 3-hour GPS location data obtained from adult female 9873R during 11 October – 1 November, 2006. Field crews searching for predation events located deer that had been killed by 9873R at the location clusters labeled A, B, and C.

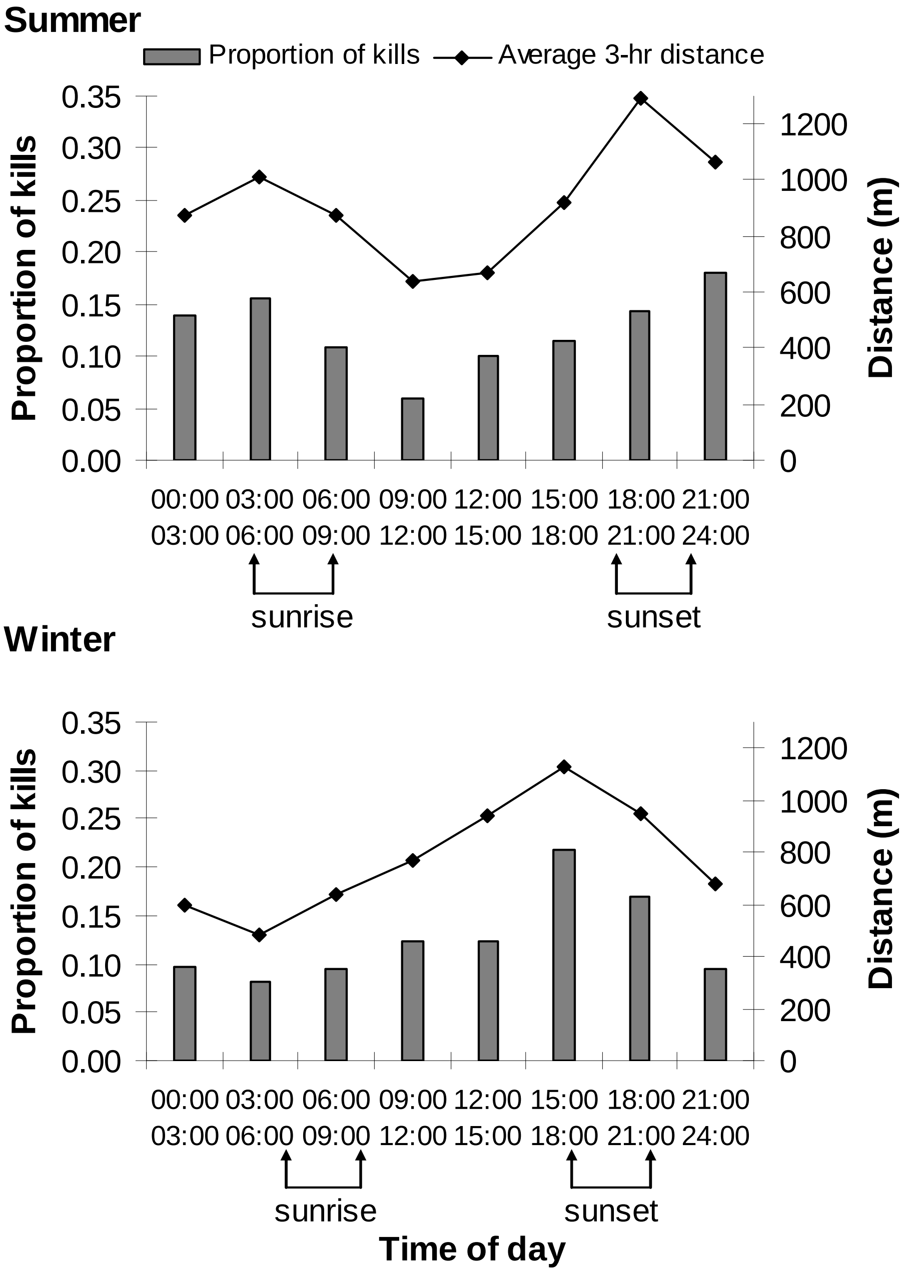

Figure 6.2: The proportion of kills made and the average step-length while searching during eight 3-hour intervals for 41 cougars in summer and winter in west-central Alberta, Canada during 2005-2008. Movement and predation are highly correlated in summer (R^2 = 0.58) and, especially, in winter (R^2 = 0.86). The arrows indicate the range of sunset and sunrise times in each season.

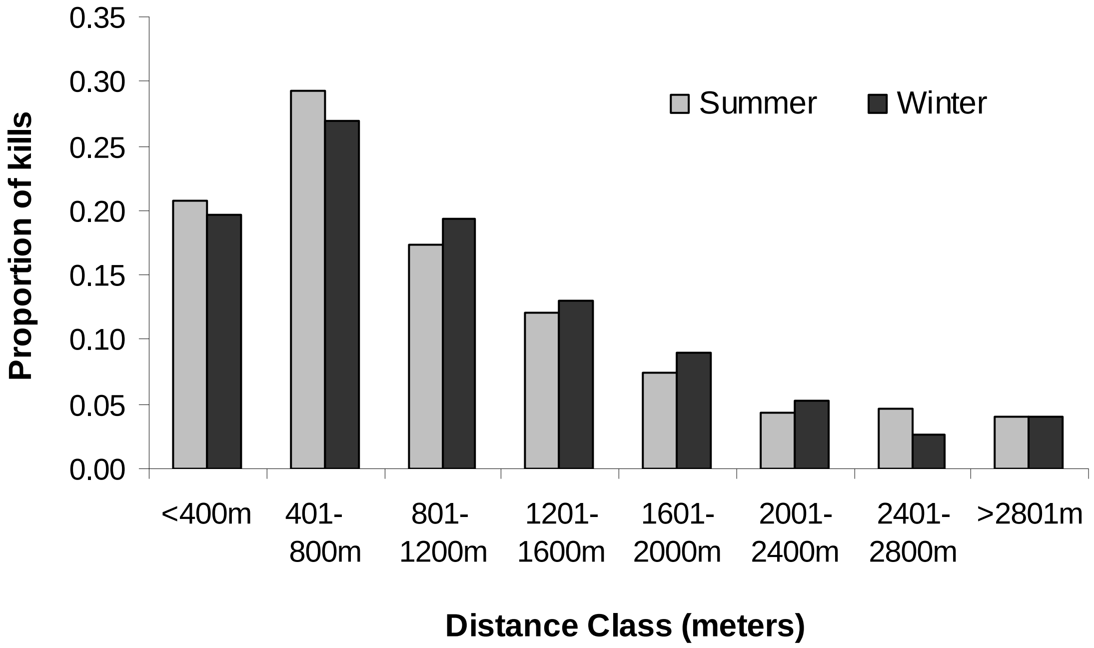

Figure 6.3: Seasonal proportion of predation events falling within 400 m distance categories representing straight line distances moved by cougars during the 3 hour period preceding the first location fix at a predation cluster for 322 predation events in summer and 300 in winter obtained from 41 GPS collared cougars in west-central Alberta, Canada during 2005-2008.

Cougars did not kill prey uniformly throughout the diel cycle in either summer ($\chi^2 = 8.46$, *d.f.* = 3, $P = 0.037$) or winter ($\chi^2 = 15.42$, *d.f.* = 3, $P < 0.001$). In both seasons, the highest proportion of cougar kills was made during the evening, while the second highest proportion was made during the day (Table 6.1). When differences in the length of the daylight period are accounted for in summer, however, cougars made kills more often than expected during the evening, overnight, and in the morning, and less often than expected during the day. During winter, cougars killed prey as expected during the day, more often than expected in the evening, and less often than expected overnight and in the morning (Table 1). Cougars also exhibited a statistically significant seasonal shift in predation patterns from more nocturnal in summer to more diurnal in winter ($\chi^2 = 10.84$, $d.f. = 3$, $P = 0.013$).

Autocorrelation functions revealed a 24-hour cycle in activity level during both summer and winter (Figure 6.4). Cougars in both seasons exhibited the strongest movement peaks in the afternoon (Figure 6.2), which may drive the consistent 24-hour rhythm in ACF values in both seasons. Despite a distinct pattern, however, correlation values were low (never exceeding 0.3) and declined steadily over time, indicating that cougar movements were only weakly autocorrelated and suggesting that diel hunting behavior is not especially predictable through time. Moreover, ACF values are substantially lower in summer than in winter (Figure 6.4), signifying that while cougar activity patterns are not especially predictable at any time of the year, they are least predictable during summer.

Table 6.1: A comparison between the number of kills expected if cougar predation occurred uniformly throughout the day and the number of kills observed in each diel period in each season for 41 cougars in west-central Alberta, Canada, during 2005-2008. The difference presented here is the percent of kills in a diel period that fall above or below the expected value.

		Time of day			
		Morning	Day	Evening	Night
Winter	Observed Kills	54	76	119	59
	Expected Kills (null hypothesis)	77	77	77	77
	Difference	- 30%	-1%	+ 55%	- 23%
Summer	Observed Kills	85	88	104	45
	Expected Kills (null hypothesis)	80.5	120.75	80.5	40.25
	Difference	+ 6%	- 27%	+ 29%	+ 12%

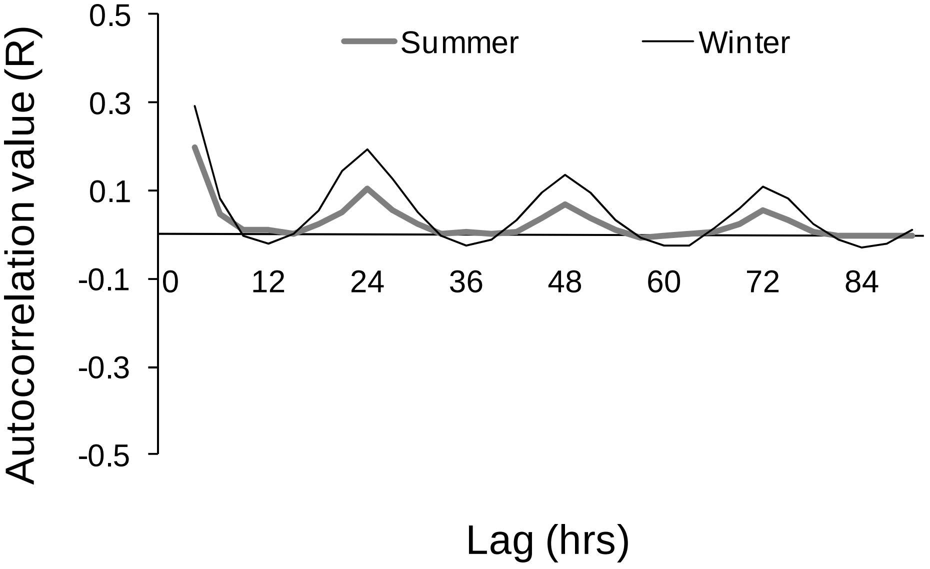

Figure 6.4: Autocorrelation functions for activity (step-length between successful 3-hr fixes) of 41 GPS collared cougars in summer and in winter in west-central Alberta, Canada, during 2005-2008.

Fix success was substantially higher for collars worn by elk, and 90% of elk movements (n = 49,861) were successfully assigned to a specific 2-hour interval. Elk in west-central Alberta were most active in the early morning and late evening during both summer and winter (Figure 6.5). They also were more active during the day than at night in both seasons. During winter, elk activity was highly concentrated within the shorter diurnal and crepuscular period, whereas in summer activity was more uniform throughout the day, possibly because of increased duration of daylight and warmer temperatures overnight. Cougar movement and predation patterns peaked in early morning and late evening in summer, matching similar peaks in elk activity, but cougars were more nocturnal than elk (compare Figures 6.2 and 6.5). Cougars in winter, on the other hand, showed a strong depression in movement and predation in the early morning (Figure 6.2) when elk activity peaked (Figure 6.5), but both cougars and elk were more diurnally active during winter and both exhibited evening peaks in activity (compare Figures 6.2 and 6.5). Comparisons between cougar activity and elk movement data adjusted to 3-

hour intervals indicate a positive relationship between elk and cougar activity levels in both seasons (Figure 6.6), but the relationship was stronger in winter (*R* = 0.70, *P* = 0.050) than in summer (*R* = 0.46, *P* = 0.213).

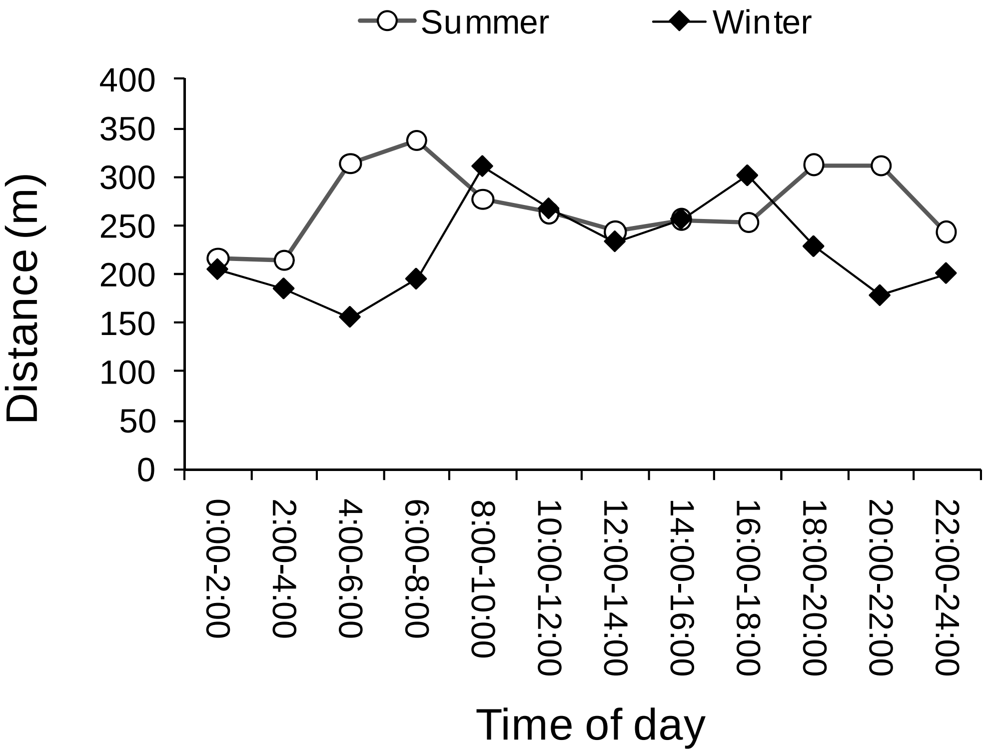

Figure 6.5: Mean distance moved during 2 hour intervals by 18 GPS radiocollared elk in summer and winter in west-central Alberta, Canada during 2000-2003.

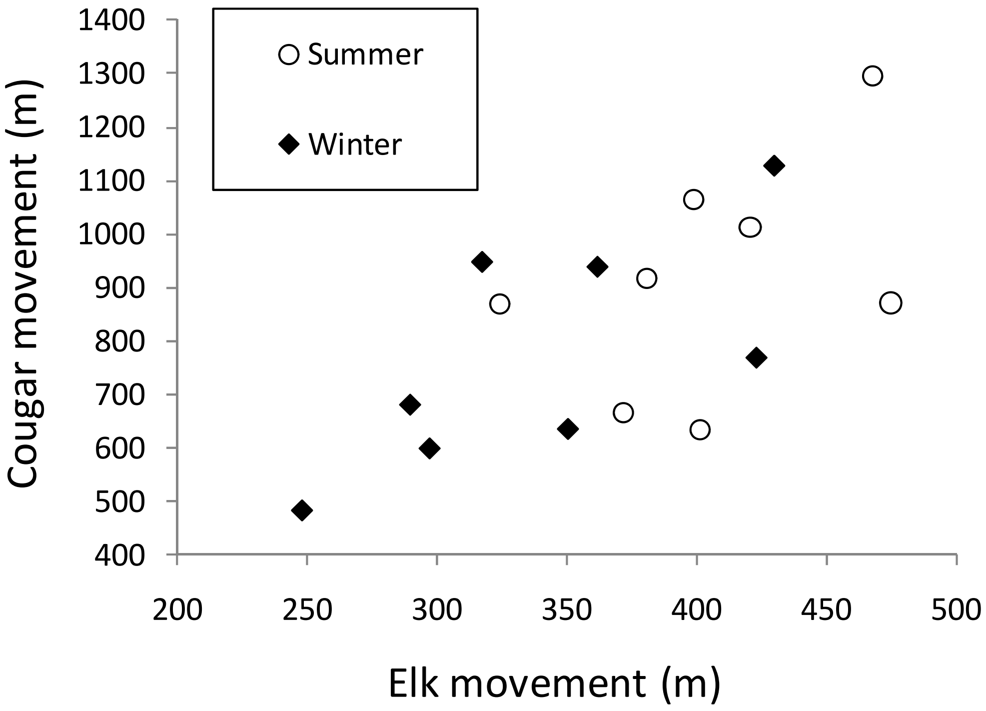

Figure 6.6: Relationship between elk and cougar movements during 3-hour intervals in summer and winter in west-central Alberta during 2000-2008.

DISCUSSION

Active vs. ambush predation

My results contradict the common assertion that cougars are ambush predators (e.g., Rominger et al. 2004, Wilmers et al. 2007, Krumm et al. 2009). High correlation between the average distance moved by hunting cougars and the frequency of predation during 3-hour diel intervals, combined with longer than average movements made by cougars in the interval immediately preceding the first location fix at a predation cluster, signifies an active hunting strategy. This does not imply that cougars never make kills from ambush, only that active predation is the dominant strategy employed by cougars in west-central Alberta. My findings are consistent with the early assessment of cougar hunting behavior given by Seidensticker (1973, p. 26), where he states that cougars "zigzagged back and forth through thickets, moved around large openings, under rock overhangs, up and down little draws, and back and forth across creeks" to locate and kill prey.

In some cases, the term ambush predator might have been applied loosely by researchers to refer to the fact that cougars attack their prey at close distances. Thus, prevalent use of the term might have injected uncertainty regarding the nature of cougar predation into the literature even though most researchers do not believe that cougars employ a sit-and-wait strategy in the traditional sense of ambush predation. Similar problems in terminology have plagued various fields of ecological study in the past, highlighting the importance of careful word choice in scientific work (Starzomski et al. 2004). The GPS telemetry approach I used in this study provides an efficient means to rigorously quantify hunting behavior for large carnivores and can help resolve termonology.

My results question assigning to cougars traits that theory associates with sit-and-wait ambush predation, such as reduced selectivity for prey and greater additive predation (e.g., Wilmers et al. 2007). Indeed, while felids in general are often qualitatively described as sit-and-wait ambush predators (Hopcraft et al. 2005), they may be less prone to using an ambush strategy than is commonly asserted. For instance, Murray et al. (1995) snowtracked lynx (*Lynx canadensis*) hunting snowshoe hares in the Yukon and found that 80% of predation attempts occurred while lynx were actively searching for prey. Unlike sit-and-wait predators that may not have the luxury of being selective and are expected to kill prey as they come into range of an ambush (i.e., as available; Wilmers et al. 2007), stalking predators are mobile and can choose which prey to approach and which to attack. Attacking prey can be a dangerous activity for a large carnivore (Sunquist and Sunquist 1989, Ross et al. 1995, Logan and Sweanor 2001) and there is no reason to expect that mobile predators with the opportunity to be selective should fail to choose to attack more vulnerable prey.

Indeed, there is little empirical support for a dichotomy in prey selection between stalking and coursing predators in large mammal predator-prey systems (Kunkel et al. 1999). When comparing the prey selection of cougars to that of wolves (*Canis lupis*), Husseman et al. (2003) suggest that a stalking and ambush hunting strategy accounted for lower degree of selectivity exhibited by cougars. However, a majority of studies have found that cougars select for more vulnerable prey (Murphy 1998, Pierce et al. 2000, Chapter 4), and, more often than not, that cougars are just as selective as their coursing canid counterparts (Kunkel et al. 1999, Pierce et al. 2000). Recent evidence further indicates that not only might cougars select for vulnerable individuals on the basis of age, size, or sex (Murphy 1998, Pierce et al. 2000), but that they may also select for individuals in a weakened condition due to reproductive behavior (Chapter 4) or to disease (Krumm et al. 2009). Stalking predators may choose to approach and attack more vulnerable individuals to reduce risks associated with predation, while coursing predators may kill less fit individuals because those individuals are easier to capture, but the resulting selection for vulnerable prey may often be similar.

Predictable vs. stochastic predation

Physiological constraints on diel hunting patterns provide predictable temporal refugia for prey, with associated implications for prey behavior, population dynamics, and ecosystem structure (Kolter et al. 1991, Fenn and MacDonald 1995, McIntosh and Townsend 1996, Kolter et al. 2002, Roth and Lima 2007). Most data on cougar hunting behavior suggest a temporal refuge for prey during the day (Beier et al. 1995, Anderson and Lindzey 2003, Sweanor et al. 2008). The pattern during winter in Alberta, however, appears to cntradict this notion, and cougar movement distances and hunting success increased during the day and peaked in the evening before declining overnight. Cougar predation in Alberta during summer yielded a pattern more similar to the results of previous studies because cougars exhibited crepuscular peaks in both activity and predation, but cougars nevertheless hunted frequently and killed substantial numbers of prey (i.e., 27%) during the day. Mattson et al. (2007) also found that > 20% of all prey killed by cougars in Arizona occurred during the day. Therefore, cougar hunting behavior appears to be more flexible with respect to ambient light conditions than is sometimes suggested (e.g., Anderson and Lindzey 2003).

Although cougar predation is not as strongly tied to a specific temporal period as if cougars were physiologically restricted to hunting at night, predation remained somewhat predictable, and cougar activity levels and predatory success maintained clear diel peaks, especially in the evening, during both summer and winter. This result is further supported by my ACF analysis, which revealed that cougars exhibit a consistent daily rhythm (24-hr period) in their movements while searching for prey. The low amplitude of the cycle (weak correlation) that decayed steadily, however, points to extensive variability in cougar hunting behavior over time (i.e., from one day to the next). Hence, although cougars exhibited broad diel activity patterns, they also maintained a considerable element of unpredictability in their hunting behavior.

This result provides initial data to help address Ferrari and Chivers' (2009) question of whether predation is inherently predictable or stochastic in natural systems. In the case of cougars, predation appears to maintain elements of both. Peaks in cougar activity might indicate focused hunting efforts at times of day when the probability of successfully killing prey is highest. Thus, just as prey adjust their behavior in predictable ways to avoid predators (Kolter et al. 1991, Fenn and MacDonald 1995, Roth and Lima 2007), cougars might predictably adjust their behavior to capture prey. But hunting throughout the diel cycle might also indicate participation in a temporal version of the spatial "shell games" proposed by Mitchell and Lima (2002), presumably as a means to manage "ratcheting" vigilance responses by prey to predictable predation (Lima 2002, Mitchell 2009). The risk allocation hypothesis suggests that vigilance behavior in prey declines as predation risk becomes constant over time (Lima and Bednekoff 1999), and because cougars can hunt throughout the diel cycle the ability of prey to trade off high vigilance during periods of high predation pressure for the ability to forage and move freely at times of low predation risk is limited by the potential for cougars to adaptively exploit periods of reduced vigilance by prey.

My data also provide support for the hypothesis that the predictable component of cougar predation is driven by prey activity. Cougar activity patterns showed a positive relationship with elk activity in both seasons, as predicted by the bottom-up hypothesis (Curio 1976, Beier et al. 1995, Karanth and Sunquist 2000). In summer cougars remained more nocturnal than elk, which may account for the weaker relationship during that season, although crepuscular peaks in activity were exhibited by both predator and prey. In winter cougars failed to match the early morning peak in elk activity with a similar peak in predation, but the overall increase in diurnal activity by cougars appears to account for the tighter relationship in that season. A possible reason that the activity patterns of elk and cougars are not more similar is that the primary prey of cougars in west-central Alberta are deer (Chapter 4), and cougars might conform more closely to their behavior than to that of elk. However, this probably does not explain the lack of a predation peak at dawn by cougars in winter because deer generally exhibit bimodal activity peaks at dawn and dusk (Halls 1984), similar to those exhibited by elk.

Within an optimal foraging paradigm (Stephens et al. 2007), it is reasonable to suppose that cougar hunting behavior maximizes benefit with respect to the behavior of primary prey and trophic competitors, producing a distinct predation pattern with peaks occurring when hunting is most profitable, but ensuring that predation remains sufficiently unpredictable to limit anti-predator responses by prey. If predators attempt to optimize their behavior with respect to primary prey, it may provide opportunities for alternate prey to exploit temporal refugia from predation pressure (e.g., the early morning peak in elk activity during winter), which might have a stabilizing influence on community structure (Hampton 2004). Additional data will be required to test these hypotheses, however. Indeed, untangling the behavioral games underlying the dynamics of complex multi-species interactions like those found in west-central Alberta remains a major challenge for ecologists, but doing so will provide an improved mechanistic understanding of observed patterns of hunting behavior and may yield a better understanding of community structure and dynamics.

Cougar-human conflict

In contrast to what has been reported elsewhere (e.g., Beier et al. 1995, Sweanor et al. 2008), cougars in west-central Alberta were not always most active at night when humans are least active. During winter, cougar activity peaked in the afternoon and evening between 12:00 and 18:00, increasing the potential for conflict with humans at this time. In addition, the stochastic component of cougar predation makes it difficult to identify a particular time of day when risk of conflict can be considered low. While humans can modify their behavior to avoid diel peaks in cougar activity and predation, my ACF analysis indicates that there is no time of day when cougars are consistently inactive, especially during summer. Thus, while early mornings in winter and the middle of the day in summer may present the lowest risk (i.e., least activity), the chance that cougars will be actively hunting at these times remains reasonably high. Consequently, although better than nothing, managing cougar-human conflict by restricting human use of cougar habitat to specific time periods (e.g., Sweanor et al. 2008) might be only minimally effective. Similarly, effective protection of livestock by attempting to account for temporal peaks and troughs in cougar activity (e.g., nocturnal sequestration of stock) is made difficult by predation that occurs throughout the diel cycle. Because cougars are most active when prey also are active, managers responsible for preventing or mitigating conflict may be able to use prey activity to index cougar activity.

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CHAPTER 7

DISSERTATION SUMMARY

As Paul Errington (1946, p. 144) famously stated: “whatever else may be said about predation, it does draw attention...” . The second part of Errington’s sentence is less often quoted and reads “…and the literature dealing more or less directly with the subject surely numbers many thousands of titles”. The attention of ecologists certainly has not waned in the decades following these remarks. A search in Web of Science (http://www.isiwebofknowledge.com) for the key word ‘predation’ in April 2010 returned 36,759 published papers, with hundreds of new titles appearing each month. Indeed, fascination with predators, especially fierce ones like large carnivores, is as old as humanity. The attention people pay to such predators is frequently negative, however, and only during the last century have western perspectives shifted to incorporate a positive opinion of large carnivores.

For thousands of years, western society viewed large carnivores as a blight on humanity. People relentlessly pursued their elimination, in many cases successfully. Since the arrival of Europeans in North America, for instance, the range of wolves (*Canis Lupus*), cougars (*Puma concolor*), and grizzly bears (*Ursus arctos*) were substantially reduced by organized, sustained, and often government sponsored persecution (Laliberte and Ripple 2004). Indeed, intense persecution did not stop until the 1960s, when new information began to shift attitudes and perspectives.

In the 1940s and 1950s, influential biologists like Paul Errington and Aldo Leopold noted that predation did not always have negative consequences. Errington (1946) showed that some animals killed by predators would not have survived otherwise (i.e., predation as compensatory mortality), while Leopold (1949) described the self-destructive devastation that deer could cause to their range when their natural predators (wolves) were extirpated. These ideas have been strongly championed since, and ecologists and conservationists have spent substantial time and effort attempting to demonstrate the positive ramification of maintaining large carnivores on the landscape (Ray et al. 2005).

However, just as it is dangerous to classify large carnivores as an evil that must be eradicated, we must take care lest they be inappropriately elevated to ecological sainthood. As Paul Beier (2009, p. 178) points out with respect to cougars (*Puma concolor*): "advocates for cougars readily accept the idea that cougars should be conserved because they are important top-down regulators. But when confronted with a proposal to reduce cougar numbers temporarily to benefit a struggling bighorn or pronghorn population, some of these same advocates deny any significant top-down role for cougars". In fact, large carnivores can be a source of extinction (Logan and Sweanor 2001, DeCesare et al. 2009) as well as of conservation (Ray et al. 2005), and it is important not to forget the devastation they are capable of causing by taking human life (Corbett 1944).

The truth about large carnivores therefore lies somewhere between the extreme views of sinner and saint, and effective management will depend on a balanced perspective that acknowledges and permits open discussion of both 'bad' and 'good' aspects of large carnivore predation. Wildlife managers are often placed in the unenviable position of trying to minimize the former and maximize the latter. Although this task is increasingly important as many species of North American large carnivore are recovering and recolinizing parts of their range from which they had previously been extirpated (Mladenoff et al. 1995, White and Garrott 2005, Miller 2007, Appendix I), it is also extremely challenging because the effects of large carnivore predation are complex and variable, and because people's opinions about carnivores also are disparate (Kellert et al. 1996). One way to improve the ability of managers to effectively conserve large carnivores and their prey is to ensure that appropriate information is available. In this dissertation I have attempted to provide managers with a better understanding of predation by one important large carnivore, the cougar, in west-central Alberta, Canada.

The scope of the topics I covered was broad, ranging from advancing methodology, to providing basic descriptive data, to testing hypotheses and evaluating theory. I began by assessing and refining techniques for monitoring cougar predation using Global Positioning System (GPS) telemetry data (Chapter 2), and applied my approach to develop the largest dataset on cougar predatory behavior collected to date. Using these data, I showed that cougars are facultative scavengers and that scavenging makes cougars susceptible to snaring at wolf bait-stations (Chapter 3), clarified the effects of season, demography, and prey vulnerability on cougar kill rates and prey composition (Chapter 4), developed and applied a multi-species functional response for cougars and assessed the prevalence and implications of prey switching and prey specialization by cougars (Chapter 5), and demonstrated that cougars are not nocturnal ambush predators (Chapter 6).

In each chapter I tried to identify and clearly articulate the management and conservation implications of my findings. Managers should be aware, for instance, that incidental snaring at wolf bait stations can be an important source of cougar mortality, that cougars kill ungulates more frequently in summer than in winter, that cougar population structure might substantially influence prey dynamics, that cougars focus on vulnerable prey, that cougars tend to select for abundant prey (prey switching) and risks to small populations of alternate prey come primarily from individual specialists, and that cougars are active and frequently hunt during the day.

Many of these conclusions were previously unclear. Indeed, they were usually contested, with arguments and theories running in opposite directions. Global Positioning System telemetry provided me with a tool to collect one of the largest datasets on cougar predation available anywhere, allowing me to settle some of the debates, and present new information (i.e., the first assessment of cougar functional response). Clearly, there is much work left to do, but perhaps now managers will have more of the details they need to make decisions when faced with incompatible theories and contrasting data. If this work improves the ability of wildlife managers to make better decisions with respect to effective conservation of cougars and their prey, I will have achieved my goal.

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APPENDIX I

NUMERICAL INCREASE AND RANGE EXPANSION OF COUGARS IN ALBERTA DURING 1991-2009

By the late 1940's and early 1950's cougars (*Puma concolor*) were extirpated from much of their original range in North America. Where they persisted, numbers were substantially reduced as a result of direct persecution by humans and because of human-caused reductions in ungulate densities (Jalkotzy et al. 1992, Cougar Management Guidelines Working Group 2005). However, several studies indicate that cougar numbers rebounded substantially after predator bounties were lifted and cougars were afforded big game status in most states and provinces during the 1960s and 1970s (Riley and Malecki 2001, Keister and Van Dyke 2002, Biek et al. 2006). Indeed, cougars are currently repopulating portions of their North American range from which they have been absent for decades (Thompson and Jenks 2007, Bacon et al. 2009).

In Alberta, Canada, a study conducted at Sheep River during the late 1980s and early 1990s indicated that the cougar population in that region was growing rapidly (Ross and Jalkotzy 1992), and a provincial estimate of 685 cougars was made in the early 1990s (Jalkotzy et al. 1992). Since that estimate, provincial human-caused cougar mortality has risen sharply from 56 cougars in 1991 to 206 in 2008 (Figure I.1). The increase has been especially steep in west-central Alberta, where human-caused mortality (mostly due to hunting and accidental snaring at wolf bait stations) has gone up by approximately 600% since 1991 (Chapter 3). Sometimes, researchers and management agencies use the number of human-cougar interactions or human-caused mortalities to index cougar population change (Keister and Van Dyke 2002). By this measure, Alberta's cougar population has grown substantially since 1991 (Figure I.1), and similar increases have occurred in most western states during the same period (Toweill et al. 2008). Breeding populations of cougars recently have been confirmed in the Cypress Hills on the Alberta-Saskatchewan border (Bacon et al. 2009), which has been viewed as an additional indication of cougar population increase in Alberta (Anderson et al. 2009).

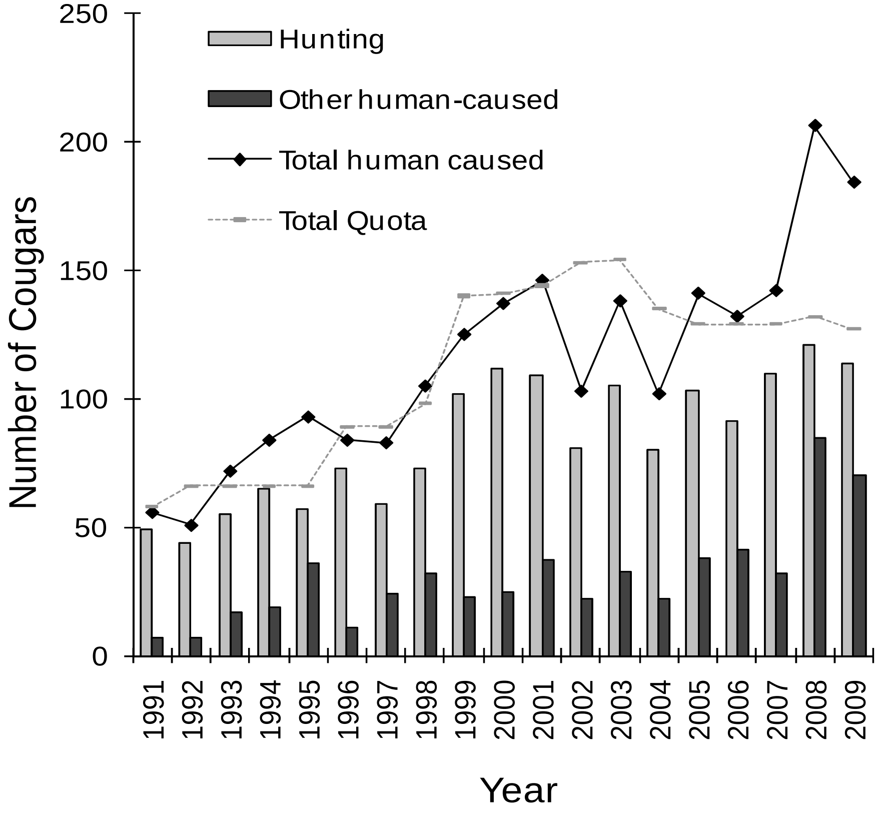

Figure I.1. The number of cougars killed by licensed hunters and other sources of incidental human-caused mortality, the total human-caused mortality, and the hunting quota in Alberta, Canada during 1991–2009. The year starts on December 1, which coincided with the first day of the cougar hunting season (i.e., 1991 includes December 1990 but not December 1991). Data supplied by Alberta Sustainable Resource Development.

However, mortality and conflict data do not always provide accurate reflections of cougar population trajectory (Cougar Management Guidelines Working Group 2005, Lambert et al. 2006). Where cougars are hunted according to a quota system, as in Alberta (Ross et al. 1996), higher mortality might be due primarily to increasing quotas (Figure I.1). Increases in incidental cougar mortality (e.g., problem cougars, roadkills, and snaring), moreover, could be explained by a rapidly growing human population and a higher potential for interaction with cougars, independent of changes in cougar density (Lambert et al. 2006). Finally, some authors have argued that increasing human-caused mortality (particularly hunting mortality) in western North America is inconsistent with maintaining viable cougar populations under current management regimes (Laundré and

Clark 2003, Packer et al. 2009), and that cougar populations have actually declined as harvest increased in many states and provinces (Lambert et al. 2006, Packer et al. 2009). Consequently, there is considerable ambiguity concerning the direction and magnitude of cougar population change at the provincial scale over the past 2 decades. Similar uncertainty surrounds cougar range expansion in Alberta. Whether the Cypress Hills were populated by cougars dispersing from burgeoning western Alberta populations or by animals moving north from Montana or North Dakota remains unclear, and while cougar distribution has expanded in central and northern Alberta (Anderson et al. 2009), trends have not been comprehensively assessed.

Uncertainty regarding cougar population trajectory with increasing cougar mortality in Alberta (Ross and Stevens 1999) and growing concern about the long-term viability of cougar populations subjected to heavy sport harvest in western North America (Lambert et al. 2006, Packer et al. 2009) prompted me to investigate cougar population change and range expansion in Alberta during 1991-2009. My primary objective was to provide a better understanding of the current status of cougars in Alberta to inform future management. Alberta's management plan for cougars, developed in 1992, delineates cougar range in 1988 and provides estimates of cougar density by Wildlife Management Unit (WMU) in all areas of the province where breeding populations were present (Jalkotzy et al. 1992). These estimates were anchored by densities obtained from intensive capture and monitoring efforts at Sheep River (Ross and Jalkotzy 1992) and were extrapolated based on track surveys and expert opinion (Jalkotzy et al. 1992). The estimates provide an historical basis for comparison with current populations.

I used data from an intensive capture and monitoring study of cougars in west-central Alberta during 2006-2007 to assess changes in cougar density, and I used data from Alberta Sustainable Resource Development (ASRD) cougar mortality database to evaluate range expansion across the province. I discuss long-term management and conservation prospects for cougars in Alberta in light of these results. In addition, because evaluating cougar population change in Alberta depends upon comparing density estimates derived from radiotelemetry census data between studies, and different techniques for estimating cougar density can cause variation in density estimates (Cooley et al. 2009), a third goal of my analysis was to compare and contrast various census-based density estimation techniques for cougars. I discuss the utility of different estimators and point out ways to ensure comparability among studies.

METHODS

Study Area and Census Techniques

I estimated cougar density in Clearwater County in west-central Alberta in 2006. My study area included provincial WMUs 318, 320, 322, 324, 326, 328, 330, 417, 418, 420, 422, 426, 428, 429, 430, 432, and 434, as well as the White Goat and Siffleur Wilderness Areas. Cougars were hunted on a quota basis (Ross et al. 1996), and the season ran from December 1 – February 28 or until the quota filled. The climate, geography, flora, and fauna of the region are described in Chapters 2-4. I selected a 294 km^2 portion of WMU 328 (centred near the town of Nordegg, Figure II.2) as a complete census area (CCA), and I attempted to capture and radiocollar all resident cougars with any portion of their home range overlapping the CCA.

The CCA was set *a priori* instead of adaptively fitted to the home ranges of captured study animals (e.g., Burch et al. 2005, Cooley et al. 2009). Cougars are not strictly territorial and to adaptively define a study area based on the composite radiotelemetry data of captured cougars can be problematic because the edges of the area will necessarily include overlapping portions of the home ranges of uncollared cougars, thereby leading to underestimates of true density. In part, I defined the boundaries of the CCA based on a well-developed network of roads and trails that allowed field crews to access the area easily and search it thoroughly. During winters 2005/2006 and 2006/2007, field crews systematically searched for cougar tracks along roads and trails within the CCA and in a buffer zone that extended approximately 5km from the CCA boundary. Partial searches were conducted haphazardly whenever snow conditions permitted, and complete surveys (i.e., all roads and trails) were methodically implemented within 72 hours of each new snowfall.

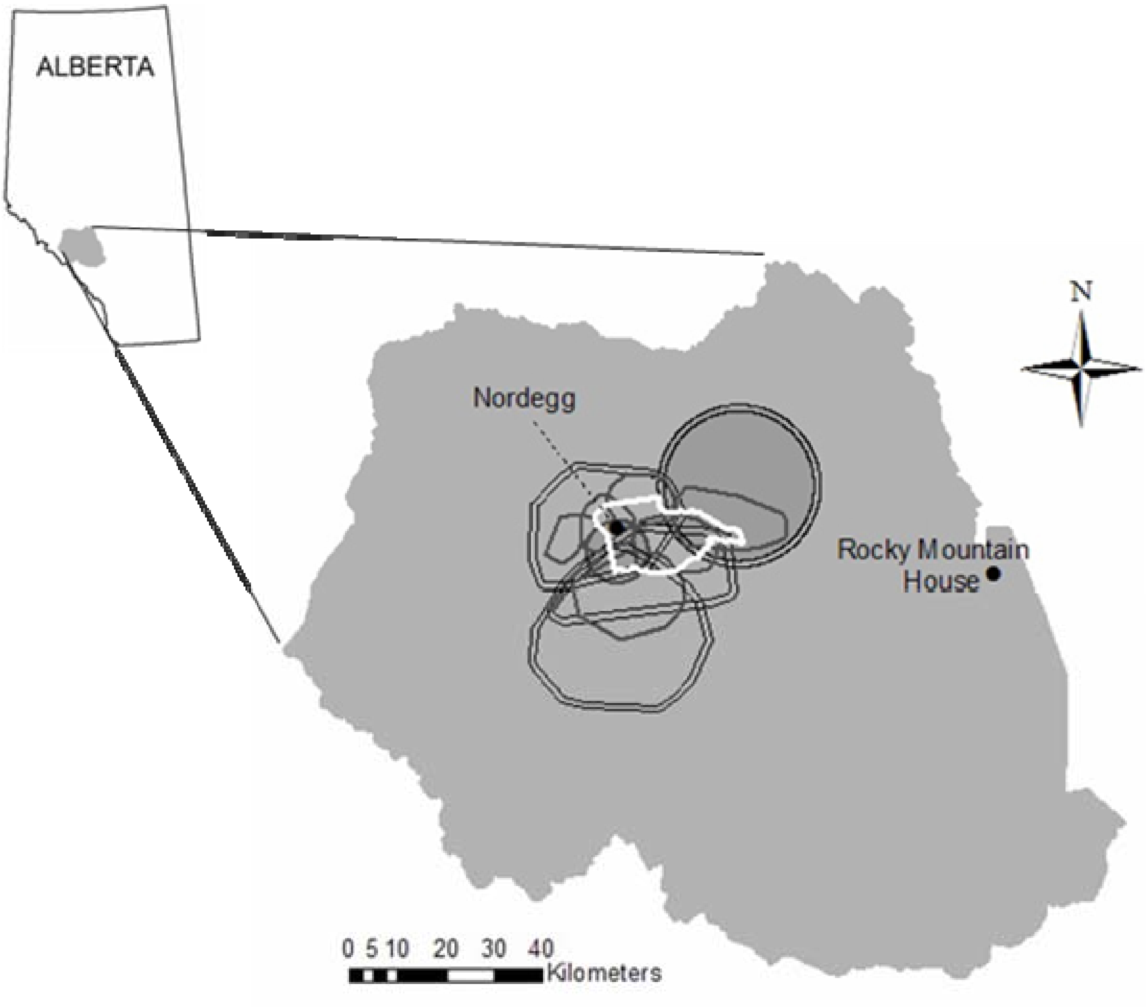

Figure I.2. Location of the complete census area (white polygon), near the town of Nordegg in west-central Alberta, Canada, with 95% minimum convex polygons of radiocollared resident males (*n* = 3, double lined polygons) and resident females (*n* = 6, thick grey polygons) present in the census area during November 2006. Also displayed are the estimated home ranges of 1 female (thick grey shaded circle) and 1 male (double lined and shaded circle), that I confirmed to be resident in the area based on tracks and other sign, but that I failed to collar.

When an uncollared cougar was located, it was pursued and treed by hounds, chemically immobilized, and instrumented with a Lotek 4400S global positioning system (GPS) collar (Lotek Engineering, Newmarket, Ontario, Canada), programmed to obtain a location fix every 3 hours and from which remote data downloads were possible. Cougars also were weighed, measured, and sexed at capture and I used a combination of tooth color and wear characteristics (Ashman et al. 1983, Shaw 1986), pelage spotting (Shaw 1986), and gum-line recession (Laundré et al. 2000) to estimate age. I assigned cougars to one of 3 age classes: kitten (still with mother), sub-adult (dispersal to 2.5-3 years), or adult (>2.5-3 years). Cougar VHF signals were monitored weekly and GPS data were downloaded fortnightly, usually from the ground but occasionally from the air during telemetry flights.

Calculating Density

Radiotelemetry census data (i.e., where all animals in a given study area are identified and radiocollared) produce the best estimates of cougar density (Cougar Management Guidelines Working Group 2005). Indeed, such estimates are benchmarks by which other population indices are evaluated (Anderson and Lindzey 2005, Choate et al. 2006). However, techniques used to calculate density from census data vary substantially in ways that might affect the comparability of results (Cooley et al. 2009). The simplest and most commonly used technique is to divide the number of cougars occurring within a study area by the study area size (e.g., Ross and Jalkotzy 1992, Anderson and Lindzey 2005, Stoner et al. 2006, Robinson et al. 2008). However, this method does not adjust for time spent outside the study area, thereby overestimating true density (McLellan 1989). This overestimation problem is akin to the edge-effect problems in mark-recapture studies (Otis et al. 1978, Bondrup-Nielsen 1983) and to problems associated with estimating study area size when calculating census-based density estimates for territorial animals using radiotelemetry (Burch et al. 2005).

Some cougar researchers have used the proportion of telemetry locations or proportion of a home range occurring within a study area to adjust density estimates (Logan and Sweanor 2001, Cooley et al. 2009). Such home-range based adjustments, also advocated by McLellan (1989) for grizzly bears (*Ursus arctos*), might solve overestimation problems and produce more reliable density estimates. However, the effect of the type of home range estimator on home-range-adjusted estimates of cougar density has not been considered. Consequently, I compared the traditional density estimation approach with home-range-adjusted approaches employing a variety of home range estimators, and use the results to improve inferences regarding numerical changes in Alberta's cougar population.

I estimated cougar density using data from all resident cougars maintaining a home range that at least partially overlapped the CCA during March to November 2006 (i.e., after the 2005-2006 cougar hunting season and prior to the 2006-2007 season). Following standard cougar density estimation procedures (Logan and Sweanor 2001, Stoner et al. 2006), adult cougars with stable home ranges captured between December 2006 and April 2007 were assumed to have been present on their home range during March-November 2006 and were incorporated into the density estimate, while sub-adult cougars < 3 years old that were potentially new immigrants into the CCA were not.

I initially estimated density by dividing the number of cougars in the CCA (i.e., residents and dependent offspring with at least a portion of the home range overlapping the CCA) by the size of the CCA. Next, I calculated home-range-adjusted density using 6 home-range estimators: 100% minimum convex polygon (MCP), 95% MCP, 85% MCP, 95% fixed kernel density estimator (KDE), 85% KDE, and 50% KDE. All home ranges were calculated using Hawth's Analysis Tools for ArcGIS (www.spatialecology.com/htools/). I estimated adult cougar density separately for each sex by summing the proportions of each radiocollared adult cougar's home range that overlapped the CCA divided by the size of the CCA to obtain a value per 100km^2. Thus, cougars with a home range completely within the CCA counted as a whole cougar while cougars with only a portion of their home range within the CCA contributed to the density estimate proportionately. Home ranges of females with kittens were multiplied by the number of cougars in the family group before summing proportions to obtain total cougar density.

For cougars known to have home ranges overlapping the CCA but that I had not radiocollared, I estimated approximate circular home ranges based on average 95% MCP home range size of other animals of the same age-sex class and located these spatially with respect to the CCA using tracks and other sign attributed to the uncollared individuals. I calculated minimum cougar densities using only home ranges estimated from GPS collared cougars, and maximum densities by incorporating estimated home ranges of both collared and uncollared cougars. For ease of interpretation, the contribution of uncollared cougars to the total density estimate was always the proportion of their estimated 95% MCP home range that fell within the CCA. I compared my density estimates to those given by Jalkotzy et al. (1992) to evaluate population growth.

Evaluating Range Expansion

I explored cougar range expansion in Alberta during 1991-2009 using provincial human-caused mortality data. Provincial legislation dictates that all human-caused cougar mortality must be reported to a Fish and Wildlife office, a regulation that has been in place since 1971. I used data from 2,176 registered mortalities where WMU was known between Dec 1, 1990 and November 30, 2009. I assigned each mortality incident to a mortality year. The mortality year started on December 1 to coincide with the first day of the hunting season (i.e., mortality year 1991 includes December 1990 and not December 1991). I used these data to map the distribution of human-caused cougar mortality in Alberta during 1991-2009. I then compared the spatial distribution of these mortalities to 623 mortalities registered between 1971 and 1990 and to the cougar abundance and distribution data given by Jalkotzy et al. (1992) prior to 1988. While mortality data may not always reflect cougar population trajectory (Lambert et al. 2006), they provide a clear indication of cougar distribution.

RESULTS

I captured 9 resident adult cougars (3 males and 6 females) with stable home ranges within the CCA during the winters 2005/2006 and 2006/2007. I also captured 2 large near-dispersal aged kittens (1 male and 1 female), 1 dispersing cougar that moved into the CCA and spent several days there before moving on, and 6 additional resident cougars with stable home ranges immediately adjacent to, but not overlapping, the CCA. The 6 adult females with home ranges overlapping the CCA were accompanied by a total of 12 kittens during March-November 2006. I identified 1 adult female (without kittens) and 1 adult male which I knew to be resident within the CCA, but which I failed to capture before their deaths in late November and early December 2006, respectively. The uncollared adult female was killed and partially consumed by a radiocollared resident male inside the CCA, while the uncollared male was shot by a licensed hunter in the buffer zone. On average, I obtained 265 days of monitoring (SD = 198) and 1,177 GPS locations (SD = 998) for each collared resident cougar that maintained a home range overlapping the CCA. The shortest monitoring period for a GPS collared resident cougar in the CCA was 25 days (126 GPS locations).

Using the raw count method, I obtained a value of 7.8 cougars/100 km^2 (i.e., 23 cougars/294 km^2 x 100), and an adult cougar density of 3.74 cougars/100 km^2 (i.e., 11 cougars/294 km^2 x 100). Home-range-adjusted methods always gave density values less than half of those based on the raw-count method (Table I.1). However, the proportion of each cougar's home range that overlapped the CCA varied by as much as 20% depending on the home-range estimator used, causing variation among range-adjusted densities (Table I.1). Estimates of total cougar density (i.e., including kittens) based on home-range-adjusted approach varied between 2.71-3.49/100 km^2, and the 50% KDE consistently produced higher density estimates than the other home range estimators (Table I.1). Density estimates for resident male cougars ranged between 0.20 and 0.34/100 km^2, while females ranged between 0.76 and 1.10/100 km^2 (Table I.1). The estimated 95% MCP home ranges of uncollared residents contributed only 0.03 (uncollared male) and 0.19 (uncollared female) cougars/100 km^2 to cougar density estimates. Thus, adding uncollared cougars to the estimates increased adult cougar densities by only 9-20% and total cougar densities by 6-8%. Adult female density was always substantially higher than adult male density, irrespective of calculation technique, but the degree to which females were estimated to exceed males did vary (range = 2.97–4.37 times male density; Table I.1). Regardless of the estimation approach I used, total cougar densities were higher than the estimate of 1/100km^2 given for the same region (i.e., WMU 328) in the late 1980s (Jalkotzy et al. 1992).

Provincial registration data indicate that cougars also have expanded their range during 1991-2009 (Figure I.3). Cougar harvest during 1970s and 1980s occurred predominantly south of the Bow River in the south-western Alberta, presumably because cougar density was much higher and human access better than in cougar range north of the Bow (Jalkotzy et al. 1992). Since 1991, however, there has been a continuing shift in the spatial distribution of human-caused cougar mortality, so that total mortalities occurring north of the Bow River exceeded 50% by 1997 and reached a high of 80% in

2006 (Figure I.4). Moreover, human-caused mortality in WMUs with estimated densities of between 0 and 0.25 cougars/100km^2 in the late 1980s and early 1990s (mostly north of the Brazeau River; Figure I.3) have increased steadily from 5% of the total provincial human-caused mortality in 1991 to 34% in 2009 (Figure I.4). Indeed, in 2008 and 2009 the number of human-caused mortalities registered in these WMUs (63 and 60, respectively) represent 78% and 74% of the 81 cougars estimated to be present in the region in the late 1980s and early 1990s (Jalkotzy et al. 1992).

Table I.1. Cougar density estimates in west-central Alberta, Canada, in 2006. Minimum densities incorporate only radiocollared animals, while maximum densities also include the approximate 95% MCP home range of 1 uncollared female and 1 uncollared male known to have home ranges overlapping the CCA. All values are given per 100 km^2.

	Home range Estimator	**Adult Male**	**Adult Female**	**All Adults**	**All Cougars**
Minimum Density	100% MCP[a]	0.20	0.78	0.99	2.71
	95% MCP	0.22	0.76	0.99	2.67
	85% MCP	0.25	0.81	1.06	2.85
	95% KDE[b]	0.20	0.80	0.99	2.75
	85% KDE	0.22	0.79	1.01	2.76
	50% KDE	0.31	0.91	1.22	3.27
Maximum Density	100% MCP	0.23	0.97	1.20	2.93
	95% MCP	0.25	0.95	1.21	2.89
	85% MCP	0.28	1.00	1.28	3.07
	95% KDE	0.23	0.99	1.21	2.97
	85% KDE	0.25	0.98	1.23	2.98
	50% KDE	0.34	1.10	1.44	3.49

[a] Minimum Convex Polygon
[b] Fixed Kernel Density Estimator

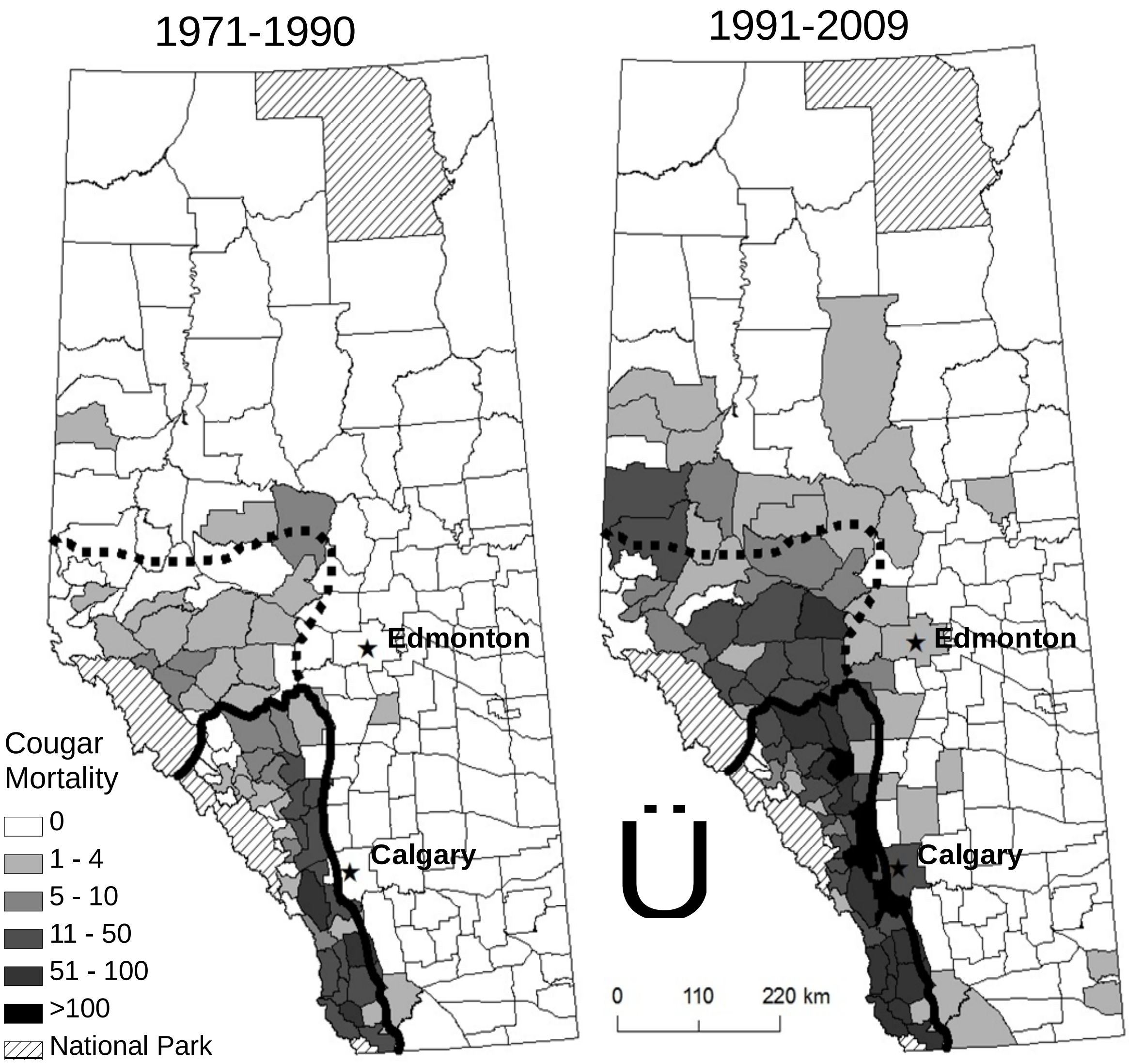

Figure I.3. Number of human-caused cougar mortalities in each provincial Wildlife Management Unit (WMU) in Alberta, Canada during 1971-1990 and 1991-2009. Also displayed are the outlines of core cougar range (1–4 cougars/100km^2; solid line) and low-density cougar range (0.1–0.25 cougars/100km^2; dashed line) for the distribution of cougars in 1988 (Jalkotzy et al. 1992). Data supplied by Alberta Sustainable Resource Development.

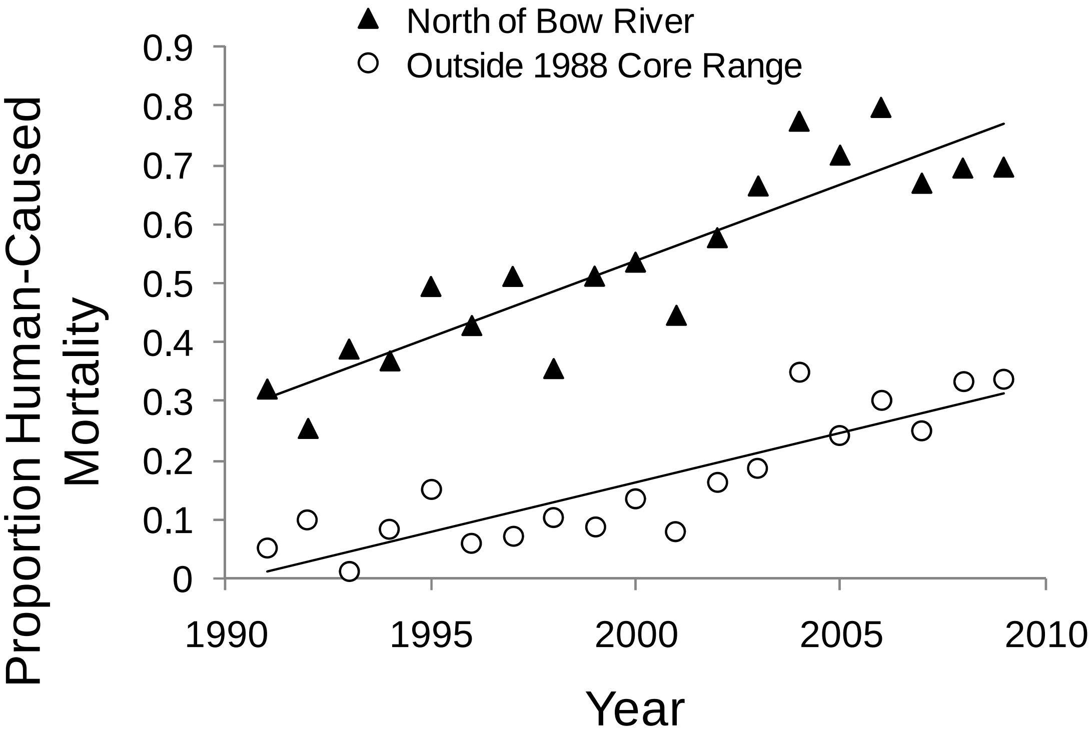

Figure I.4. Changes in the proportion of total annual human-caused cougar mortality occurring north of the Bow River and outside core cougar range (i.e., in Wildlife Management Units where cougar density was between 0.1–0.25 cougars/km^2 identified by Jalkotzy et al.1992) during 1991-2009 in Alberta, Canada. Least-squares linear regression line is displayed for each region. Data supplied by Alberta Sustainable Resource Development.

Since 1991 a total of 117 cougars (55 males, 53 females, and 9 of unrecorded sex) were killed outside the provincial cougar distribution described by Jalkotzy et al. (1992). Nine cougars were registered in these same areas during 1971-1990. The number of cougars killed annually outside these boundaries remained stable around a mean of 2 cougars between 1991 and 1999, but then increased steadily during 2000-2009 (Figure I.5). In part, this might be due to regulation changes permitting landowners to shoot cougars on private land after 2006. Nevertheless, the provincial government registered 22 cougars in WMUs located outside of 1988 range boundaries in each of the 2008 and 2009 mortality years.

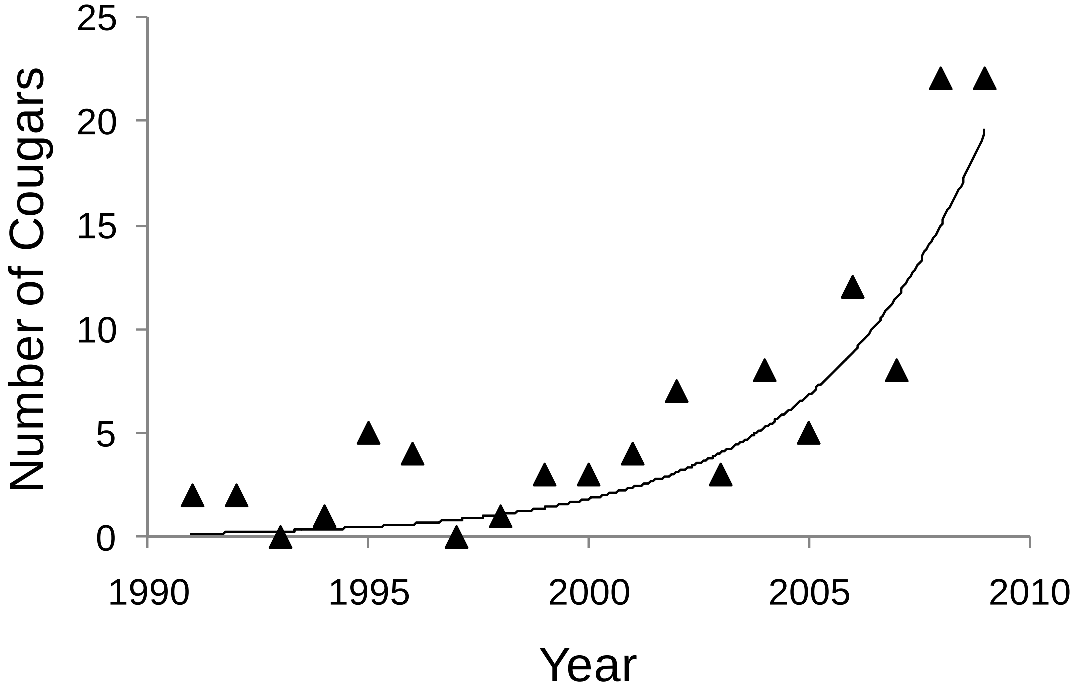

Figure I.5. Changes in the number of human-caused cougar mortalities occurring 1991-2009 outside the 1988 cougar range boundaries identified in Alberta's cougar management plan (Jalkotzy et al. 1992) during in Alberta, Canada. The best fit exponential function also is displayed. Data supplied by Alberta Sustainable Resource Development.

DISCUSSION

Cougar Density Estimation

I show that the raw-count method, which has been widely used to estimate cougar density (e.g., Ross and Jalkotzy 1992, Anderson and Lindzey 2005, Stoner et al. 2006, Robinson et al. 2008), can inflate density estimates because it includes as whole animals cougars with home ranges mostly outside the study area. In my study area, the severity of the overestimate is probably related to the small size of the CCA, within which no cougar's home range was completely subsumed, regardless of home-range estimation technique used. Larger study areas that include the entire home ranges of more animals will overestimate less severely (Bondrup-Nielsen 1983). Census-based density estimates assume a complete enumeration of cougars within the study area, however, and this assumption probably can be met only in smaller study areas (e.g., <800 km^2). Consequently, a home range-adjusted approach to density estimation should always be favored over raw counts to avoid bias.

Because the degree to which raw-count densities are inflated is unknown and depends on a number of factors such as the spatial distribution of cougar home ranges and study area size, comparing density estimates among studies employing this approach is challenging. Indeed, even recent claims that densities based on raw counts provide comparable results among temporal periods when a study area remains static (Robinson et al. 2008, Cooley et al. 2009) may be inappropriate. If the configuration of cougar home ranges shift over time as individuals die or disperse and new individuals enter the population, it is possible that different numbers of cougars will have home ranges overlapping a study area, even though landscape level densities (i.e., calculated adjusting for home ranges) do not change. Thus, a home range adjusted method might be the best way to produce comparable estimates of cougar density.

Even when cougars are enumerated using a home-range-adjusted method, however, I found that choice of a home-range estimator influenced density estimates. Consequently, while measures of uncertainty are not normally associated with census-based density estimates, reporting the range of estimates derived from different home range estimators might be applied for this purpose, especially when study areas are small relative to cougar home ranges and/or limited telemetry data are available for some individual animals. If different home range estimators produce disparate results, then researchers must be less confident in their estimates, or be prepared to defend the selection of one home range estimator over another. If density estimates remain reasonably consistent irrespective of the home range estimator used, on the other hand, researchers might place increased confidence in the estimates.

Numerical Increase and Range Expansion in Alberta

The cougar densities I estimated in west-central Alberta in 2006 exceed the estimate of 1 cougar/100km^2 given for the same region in the late 1980s and early 1990s by Jalkotzy et al. (1992), suggesting that population density has increased. The amount by which the density is estimated to have increased varies greatly, however, depending on the calculation technique selected to estimate cougar density. As noted above, an increase of 780% estimated using the raw-count method probably represents a substantial overestimate of true population growth in west-central Alberta. Although Ross and Jalkotzy (1992) also used a raw count approach, the overestimate at Sheep River should have been less than in my study because the Sheep River study area was larger. Nevertheless, home-range adjusted methods in west-central Alberta still yield estimated increases of 267%–349% (Table I.1), indicating either that cougar population density has increased, or the original density estimates were low.

Jalkotzy et al. (1992, p.35) consider density estimates they made north of the Bow River to be crude, highlighting that underestimates in the late 1980s and early 1990s might have contributed to apparent population growth. Despite being crude, however, density estimates north of the Bow River were based on track abundance, houndsmen surveys, and other expert opinion, which was calibrated by known densities at Sheep River (Jalkotzy et al. 1992). In the early 1990s, the Sheep River estimates were approximately 4 times higher than those suggested for WMU 328, while the high end of the home-range adjusted estimates that I obtained 16 years later were only slightly below the original Sheep River values, even though Sheep River estimates and subsequent provincial extrapolations would have been biased high by a raw count approach (Ross and Jalkotzy 1992). Although track surveys have low power to detect cougar population change of <50%, a difference of >400% between Sheep River and west-central Alberta should be relatively easy to detect, even with limited field investment (Beier and Cunningham 1996). It is likely, therefore, that the population changes reported here are valid and not due to failure on the part of Jalkotzy et al. (1992) to adequately characterize cougar abundance north of the Bow River.

In addition to higher cougar density in west-central Alberta, there also is evidence that breeding cougar populations now occur outside of the range boundaries delineated by Jalkotzy et al. (1992). Although cougars were sometimes observed outside these boundaries prior to 1990, observations were rare and considered extralimital (Jalkotzy et al 1992). In 2007, however, a breeding population was confirmed in the Cypress Hills Inter-Provincial Park, over 200 km from the nearest edge of the estimated 1988 distribution (Bacon et al. 2009). Whether or not WMUs adjacent to the north and eastern edges of the range delineated by Jalkotzy et al. (1992) now support breeding populations is less clear, but the frequency with which cougars are being killed in many of these WMUs combined with the fact that a large number of these individuals are females, which do not typically disperse long distances (Logan and Sweanor 2001), suggests breeding populations are present. Certainly in WMUs 356 and 357 near the city of Grand Prairie where 20 human-caused cougar mortalities were reported over 2 years in 2008 and 2009, the evidence for an established breeding population is compelling.

The human-caused mortality data used to estimate range expansion will underestimate the occurrence of breeding cougar populations in WMUs where there is little human presence (e.g., in many northern WMUs). Even in the Cypress Hills (surrounded by WMUs 118 and 119), where a breeding population occurs at high density and recreational and agricultural use by humans is extensive (Bacon et al. 2009), only 5 human-caused cougar mortalities were reported during 1991-2009. Consequently, the distribution of cougar mortalities during 1991-2009 in Figure I.3 should be considered a conservative indicator of current cougar distribution. Jalkotzy et al. (1992), for example, included a number of WMUs where no cougar mortality was reported during 1971-1990 into their estimate of provincial cougar distribution (Figure I.3).

My results are inconsistent with Packer et al.'s (2009) suggestion that increasing cougar harvests reported for many states and provinces over the last 25 years are indicative of over-harvest that poses a serious threat to cougar conservation. Packer et al. (2009) are correct that sport hunting can create population sinks and cause cougar population decline (Anderson and Lindzey 2005, Lambert et al. 2006, Stoner et al. 2006, Robinson et al. 2008), and some authors have expressed concern that rising cougar mortality in Alberta during the 1990s might not have been sustainable (Ross and Stevens 1999). Indeed, a combination of sport hunting and incidental snaring by trappers probably was sufficiently high during 2005-2008 to produce a population sink in part of west-central Alberta (Chapter 3). Yet, data from the broader provincial scale indicate that hunter harvest and other sources of human-caused mortality increased in tandem with cougar population growth and range expansion during 1991-2009.

Packer et al. (2009) argue that peaks followed by declines in hunter harvest in many US states indicate cougar population decline. In some states, however, cougar populations may have declined from highs during the 1990s as a result of management agency responses to increasing attacks on livestock, pets, or people, or to reduce predation on vulnerable ungulate populations (Rominger et al. 2004, Lambert et al. 2006, Oregon Department of Fish and Wildlife 2006, Nadeau 2008, Utah Cougar Advisory Group 2009). Using Packer et al.'s (2009) reasoning that cougar mortality patterns track population trends, moreover, total harvests still represent a substantial population increase over post-bounty era numbers, even after harvests declined from peak values (see Figure 2 in Packer et al. 2009). During the bounty years, for instance, cougar numbers were so low that fewer than 5 were killed annually in Montana between 1925 and 1930 (Riley et al. 2004). By 1998 the total legal harvest in Montana reached 776, and even though this declined to closer to 300 cougars in 2006, harvest trends suggest cougar populations remained dramatically higher than during bounty years (Hornocker 2009).

Moreover, the decline in human-caused mortality in recent years in some US states, including Montana, is due in part to tighter quota restrictions intended to stabilize cougar populations and prevent overexploitation (Apker 2008, Williams 2008), decoupling mortality patterns and population trends. Thus, the overall picture emerging from the data I present here, the data presented in a number of other studies (Riley and Malecki 2001, Keister and Van Dyke 2002, Biek et al. 2006), and even the evidence given by Packer et al. (2009) is one of increasing and expanding cougar populations throughout northwestern North America, especially during the past 20-30 years, with some US states attempting to cap or reduce cougar populations through management action in the last decade. Contrary to a looming crisis caused by sport hunting, therefore, the weight of evidence overwhelmingly indicates broad-scale conservation success for cougars in western North America.

Cougar populations are thought to be driven largely by prey abundance (Pierce et al. 2000, Logan and Sweanor 2001, Laundré et al. 2007); hence changes in cougar distribution and abundance in recent decades may not only be due to careful harvest management, but might also reflect changes in ungulate populations (Riley and Malecki 2001, Hornocker 2009). In Alberta, deer are the most important species in cougar diets (Ross and Jalkotzy 1996, Chapter 4) and therefore contribute most to cougar numerical response. White-tailed deer (*Odocoileus virginianus*), in particular, have increased throughout North America in recent decades (Roseberry and Woolf 1998, Brown et al. 2000, Cooley et al. 2008), possibly in response to better habitat created by agriculture and industry (Roseberry and Woolf 1998) and because of climate change (Johnston and Schmitz 1997). Researchers and management agencies continue to document increasing and expanding white-tailed deer populations in western and northern Alberta (Latham 2009, Webb and Anderson 2009). White-tailed deer are the primary prey of cougars in west-central Alberta (Chapter 4), and it seems reasonable to hypothesize that increasing numbers of white-tailed deer contributed to cougar population growth in that region, and that white-tailed deer expansion northward also might facilitate cougar expansion into higher latitudes. Indeed, white-tailed deer are now present in the Yukon and Northwest Territories (Hoefs 2001, Veitch 2001) and, at least occasionally, so are cougars (Jung and Merchant 2005).

MANAGEMENT IMPLICATIONS

Increasing and expanding cougar populations in Alberta will serve to improve conservation prospects for the species. However, these changes also come with considerable implications for managing ungulate prey and human-cougar conflict. Several studies have highlighted the potential for cougars to negatively impact populations of secondary prey such as mule deer, bighorn sheep, and caribou via apparent competition (Kinley and Apps 2001, Robinson et al. 2002, Rominger et al. 2004). The expansion of white-tailed deer and cougars in Alberta might intensify the effects of apparent competition for some species of alternate prey, particularly woodland caribou that are declining in Alberta (Dzus 2001) and might be especially susceptible to the predator-mediated decline (Bergerud and Elliott 1986, Latham 2009). Moreover, simultaneous increases in both cougar and human populations in Alberta will increase opportunity for human-cougar conflict, the reduction of which is an important objective of wildlife management agencies (Cougar Management Guidelines Working Group 2005). Careful monitoring of cougar population growth and (re)colonization of the province by the various provincial agencies involved in wildlife research and management should facilitate the identification and mitigation of the ecological and social issues that will accompany numerical increase and range expansion.

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APPENDIX II

DELAYED CAPTURE-RELATED MORTALITY AND LONG-TERM CAPTURE EFFECTS IN COUGARS

For many species of wildlife, effective management and conservation depends on information that can only be obtained by capturing, handling, and marking individual animals in their natural habitat. Marking in the form of wildlife telemetry has proven particularly important, especially for those species which are elusive, occur at low densities, or range over vast areas. In the case of large terrestrial mammals, for example, advances in telemetry technology have made it possible to study many aspects of ecology and behavior that would otherwise be impossible to investigate (Messier et al. 1992, Johnson et al. 2004, Sand et al. 2008). Accordingly, capturing large mammals to deploy telemetry collars has become a standard research practice.

The practice of handling and marking wildlife is not cost-free, however; capture can have significant consequences for study subjects. Injury and mortality occurring as an immediate result of physical restraint or anesthetic complications are easily detected and often reported (Logan et al. 1999, Arnemo et al. 2006). Other consequences of capture and marking such as delayed capture-related mortality (Beringer et al. 1996, Cattet et al. 2008b), reductions in post-capture survival (Jackson and Wilson 2002), and sub-lethal behavioral and physiological effects (Zann 1994, Cattet et al. 2008a) are much more difficult to detect, but can have substantial implications for animal welfare and the interpretation of research results. In terms of animal welfare, mortality rates exceeding 2% are considered unacceptable for research projects involving large mammals (Arnemo et al. 2006); delayed capture related mortalities need to be identified and included in calculations of total mortality, but may go undetected if the time between capture and mortality is long. From a research perspective, failure to detect the effects of capture or marking on survival or behavior can lead to poor inferences about population dynamics (Gauthier-Clerc et al. 2004), life history characteristics (Coté et al. 1998), and behavioral ecology (Brooks et al. 2008), impairing science and conservation.

Identifying and minimizing the effects of capture on animals are therefore important tasks for wildlife researchers. For large carnivores, however, the long-term effects of capture have generally been ignored (i.e., they are infrequently discussed and implicitly assumed by researchers to have little effect on the data collected from marked animals). This may be due to either the stigma or difficulty associated with identifying such effects. In the rare cases where careful evaluations have occurred, there is evidence both for (Cattet et al. 2008a) and against (Creel et al. 1997) lasting effects of capturing and collaring carnivores.

In this appendix, I report on 4 cougars (*Puma concolor*) that were apparently healthy when they were captured for research purposes in west-central Alberta, but were found dead and severely emaciated 24-51 days later. Emaciation and death due to disease or starvation occurs naturally in many cougar populations (Ross and Jalkotzy 1992, Logan and Sweanor 2001), and I documented 2 cases of severe emaciation which lead to death in un-collared cougars during my study. However, due to the temporal proximity of the 4 starvation mortalities of collared cougars to the capture event and the rapid deterioration in body condition post-capture, I could not unambiguously rule out capture as an aggravating cause of death. Consequently, I tested the hypothesis that the mortalities I observed resulted from the capture and collaring procedure. In addition, because of the potential importance of sub-lethal effects of collaring for the interpretation of research results (Cattet et al. 2008a), a second goal of my analysis was to explore the possibility that cougars that did not die of emaciation altered their behavior as a consequence of capture and collaring. Specifically, my aim was to examine the possibility that cougars generally display a post-capture depression in movement and predation, which could lead to death in extreme cases and would have serious ramifications for the analysis and interpretation of data obtained from cougars instrumented with telemetry collars.

METHODS

I conducted 57 captures of 44 cougars during 2005-2008 as part of a large-scale study of cougar ecology in west-central Alberta, Canada. My study area encompassed 16,900-km^2 of mountains and foothills and was centered approximately at 52°18’N, 115°48’W. Details of the topography, climate, flora and fauna of this region have been described elsewhere (Chapters 2-4). Capture was accomplished during winter by identifying fresh cougar tracks in the snow and pursuing and treeing cougars using hounds. Once treed, I chemically immobilized cougars using intramuscular remote drug delivery (Pneu-Dart Inc., Williamsport, Pennsylvania, USA) at an intended dose of 3 mg/kg zolazepam-tiletamine (Telazol®, Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and 2 mg/kg xylazine (Rompun®, Bayer, Inc., Toronto, Ontario, Canada). I recorded cougar pulse, respiratory rate, and rectal temperature at the onset of handling and at regular intervals thereafter (every 5–15 minutes).

I sexed, weighed, measured, and fitted each cougar with either a Lotek 4400SGPS collar (Lotek Engineering, Newmarket, Ontario, Canada, n=46 captures), a H.A.B.I.T VHF/GPS collar (H.A.B.I.T locator systems, Victoria, British Columbia, Canada, n=6 captures), or a Lotek LMRT VHF collar (n=5 captures). All collars were equipped with mortality sensors, and GPS collars were programmed to attempt a location fix every 3 hours. Collars weighed ≤ 620g and represented 0.51% - 1.66% of cougar body mass at capture. The entire handling procedure took < 1 hour and at its completion cougars were given 0.125mg/kg yohimbine (Yobine®, Lloyd Laboratories, Shenandoah, Iowa, USA) to reverse the effects of xylazine, and were released. No cougars were killed or significantly injured during the capture and handling procedures. Captures were conducted in accordance with the University of Alberta animal care protocol 479505 and under the authority of the Province of Alberta Collection and Research Permit 19872 CN.

After collaring a cougar, I attempted to locate it using radiotelemetry on the ground or from fixed-winged aircraft at least once per week to confirm mortality status (alive/dead). I identified mortality signals and recovered the remains of 4 emaciated cougars that died ≤ 51 days post-capture. I was able to assign the date of death precisely using data associated with the first GPS location occurring at the mortality site. In all cases, I identified mortality signals within 3 days of death and recovered carcasses between 1 and 8 days postmortem. All animals died near the end of winter and carcasses were cold or partially frozen when recovered. None had been subject to scavenging. Each animal was weighed immediately upon recovery and then frozen whole until it could be transferred to the lab and thawed for necropsy.

Gross necropsies were conducted on all 4 cougars by wildlife disease specialists at the government of Alberta (2 cougars), by myself (1 cougar), or by veterinary staff at the Calgary Zoo (1 cougar). Cougars were carefully examined for any injuries related capture, and darting locations were inspected especially thoroughly. Skeletal muscles were inspected for swelling or paleness that might be associated with exertional myopathy (Cattet et al. 2008b), and all internal organs were examined for macroscopic signs of disease. The gastro-intestinal track and fecal matter was thoroughly scrutinized for parasites. Fecal samples were also analyzed for Cryptosporidium and Giardia. Complete histology was attempted only for the final cougar once I began to suspect that the deaths might be related to capture and collaring. For this individual, the veterinary staff and the Calgary Zoo took sample tissues from the brain, lungs, heart, liver, kidneys, skeletal muscles, and nerves to search for microscopic indicators of pathology or disease. Intra-cardial blood samples were also taken to test for the presence of diseases such as Feline Immunodeficiency Virus (FIV) and feline parvovirus.

To further elucidate the circumstances surrounding death, I tested for differences in movement and foraging behavior between collared cougars that survived and those that died of starvation. I calculated movement rates (m/hour) based on the straight line distance between consecutive 3-hour location fixes. I then compared average distances traveled by the cougars that died with those obtained from the first 51 days of surviving cougars of the same age, sex, and reproductive status. I used 51 days because this was the maximum time that cougars that succumbed to starvation survived. I used an identical approach to compare kill rates of emaciated cougars with those that survived. I monitored predation continuously for each GPS collared cougar as long as the collar continued to function by visiting clusters of GPS locations on the ground to identify predation and scavenging events (Chapter 2). Kill rate was calculated in kg/day based on the estimated live weight of each prey item (see Chapter 4 for additional details). I used t-tests to evaluate the statistical significance of any differences found in comparisons of movement and kill rate.

In one exceptional case, I was able to continuously monitor the predatory behavior of a cougar for 62 days prior to collaring her. This was possible because I had GPS collared one of her large dependent kittens (> 10 months old). Large kittens move from kill to kill with their mothers, creating GPS location clusters at predation sites and allowing me to obtain a kill rate for the female prior to collaring. Twenty-four days after

I collared her, the adult female (9898R) succumbed to starvation. This provided me with a unique opportunity to compare cougar predatory behavior before and after the collaring event in a case where death occurred.

In addition to exploring potential causes of death for emaciated cougars, I also evaluated the possibility that surviving cougars may have experienced sub-lethal capture effects manifested by the depression and subsequent recovery of movement or predatory behavior post-capture, similar to what Cattet et al. (2008a) found in grizzly bears (*Ursus arctos*). Cattet et al. (2008a) used a modeling approach to control for habitat differences between home ranges as well as differences in behavior by sex and age when exploring the hypothesis that capture depresses the movement of black and grizzly bears. A simpler way to control for differences between individuals is to calculate the average movement rate for each animal and then use proportions (i.e., daily movement/average movement) when combining individual movement time-series to evaluate a population level response. The null hypothesis in this case is that the average proportional movements of cougars do not differ from 1 across the selected post-capture time-series (i.e., no post-capture depression and subsequent recovery). The alternative hypothesis is that movements are depressed post-capture (proportional movement <1) with either a linear or asymptotic increase over time. I evaluated these hypotheses by conducting regression analysis of the proportional daily movements of all surviving cougars from 1 to 100 days post-capture.

Because cougars kill relatively infrequently and inter-kill intervals are variable, kill rates must be estimated over long periods of time (Chapter 2). Thus, it was not possible for me to evaluate potential kill rate depression using daily values in the same way I analyzed movement data. Instead, I selected the maximum survival time of cougars that succumbed to post-capture starvation (51 days) as a cutoff and compared kill rate over this initial period with the post-51-day kill rate for each surviving cougar that was monitored ≥70 days. Comparisons were made at the population level and for the various age-sex classes (AM, AF, SAM, SAF, and family group) independently. I used paired t-tests to evaluate statistical significance of observed differences in all sets of comparisons.

RESULTS

The mortalities of cougars dying of starvation occurred at 24, 49, 50, and 51 days post-capture. Each of these animals was severely emaciated upon recovery (Figure II.1), having lost between 42% and 48% of capture bodyweight. All cougars that suffered this form of mortality were mature adult females (> 4 years) and were considered to be in prime condition at capture based on visual and hands-on assessment. I confirmed the presence of large kittens traveling with the females in 3 cases (i.e., kittens were treed with the mother) and strongly suspect their presence in the 4th case (based on snowtracking from the day prior to capture), even though the kittens were not with the female when I caught her. In each case, the capture appeared to go smoothly. With the exception of darting injuries, cougars were not physically injured during capture, nor did they have any significant pre-existing injuries that might have produced complications. Rectal temperatures (39.2 – 41.1 C), pulse rates (80 – 100 beats/min), and repertory rates (16 – 36 breaths/min) during anesthesia were stable and similar to those observed in cougars that did not die of starvation.

Necropsy revealed no evidence of exertional myopathy, which is a common cause of delayed capture-related mortality reported in wildlife studies (Beringer et al. 1996, Cattet et al. 2008b). Moreover, any injuries associated with darting were well healed by the time the cougars died and no other significant injuries or gross pathologies were present. The collars worn by emaciated cougars were loose because of the substantial weight loss suffered by the animals, but there was no obvious reason why the collars might have prevented cougars from killing or eating. Parasite loads in all cases were low, although a few roundworms (Nemetoda) and tapeworms (Cestoda) were found in the digestive tracts of 3 individuals. Analysis of fecal samples for Cryptosporidium and Giardia produced no significant findings. Gross findings supported minor gastric hemorrhage and digested blood in the intestine and feces (melena), which was probably induced by the stress of emaciation. Histology results for the final cougar identified no significant lesions within skeletal muscle, nerves, brain, or other organs. Lymphoid depletion was mild and this finding is consistent with death due to starvation and inconsistent with the presence diseases such as FIV. However, I failed to acquire serviceable serum from previously frozen carcasses (blood cells had lysed) and thus was unable to obtain conclusive results with respect to the possible presence of FIV.

Figure II.1: An adult female cougar (9898R) found dead and severely emaciated 24 days after she was chemically immobilized and fitted with a Lotek 4400S GPS collar. This cougar weighed 43 kg and was apparently healthy at capture, but weighed only 25 kg when I recovered her, representing an average loss of 0.75kg of body mass per day post-collaring.

The average post-capture movement rate for emaciated cougars (168m/hr) was no different from movement rate over the first 51 days for surviving adult females with kittens (153m/hr; $t = 0.572$, $df = 12$, $P = 0.570$). The average kill rate of 2.6 kg/day by emaciated cougars, on the other hand, was substantially lower than the 10.3 kg/day, on average, killed by surviving adult females with kittens over the first 51 days post-capture ($t = 4.04$, $df = 12$, $P = 0.002$). When I visited kills at GPS location clusters made by cougars that died of starvation, it was clear that the prey items had been consumed by cougars (evidence of characteristic carcass burial between feeding bouts and the presence of large latrines filled with cougar scat), but it was not clear how much was consumed by collared females and how much might have been consumed by their kittens. Three cougars made at least one kill between capture and eventual starvation and they probably consumed some meat, since they survived twice as long (49, 50, and 51 days) as the cougar that made no kills post-collaring (24 days).

Over the 62 days of kill rate monitoring for adult female 9898R prior to collaring her, she killed 10 deer and one coyote, averaging 11.7 kg of prey per day. She shared this prey with her two near-dispersal age and previously radio-collared kittens (one 59 kg male and one 37 kg female). After collaring 9898R, she lived an additional 24 days and made no kills. Over the 24 day post-capture period, 9898R's kittens remained at a rendezvous site which 9898R rarely visited. After 9898R's death, I deposited the carcass of a road-killed white-tailed deer at the rendezvous site. The kittens consumed the deer together and then became independent within their mother's home range, followed rapidly by dispersal. Both survived.

Regression analysis revealed a statistically significant positive slope (slope = 0.0039, $p < 0.001$) between the daily proportion of the average 100-day post-capture movements and the day since capture (Figure II.2). This slope yields a 39% increase in movement over the first 100 days post-capture. However statistical significance is driven by large sample size, and the amount of the total variation explained by the regression ($R^2 = 0.008$) is biologically unimportant. Figure II.2 provides a graphic interpretation, showing that the 95% confidence intervals surrounding the mean daily proportion of the 100-day average movement for each individual cougar over the first 100 days post-capture nearly always overlapped 1. Thus, while cougars tended to move proportionally further as the day since collaring increased, the relationship between movement and time post-collaring is so weak that I cannot conclude that collaring caused a long-term depression of cougar movements.

A short-term depression in movement, on the other hand, was evident during the first two days post-capture, and the upper limit of the 95% confidence intervals surrounding the proportion of average movement fell well below 1 (Figure II.2). I attribute other failures of 95% CI to overlap 1 (e.g., day 58 or 64) to the coincidental fact that multiple cougars happened to be hunting or on a kill on those particular days, and not to any effect of collaring. I also failed to detect any statistical differences in kill rates between the first 51 days post-capture and the rest of the monitoring period for individual cougars, although sub-adults tended to have lower kill rates during the initial post-capture period (Table II.1).

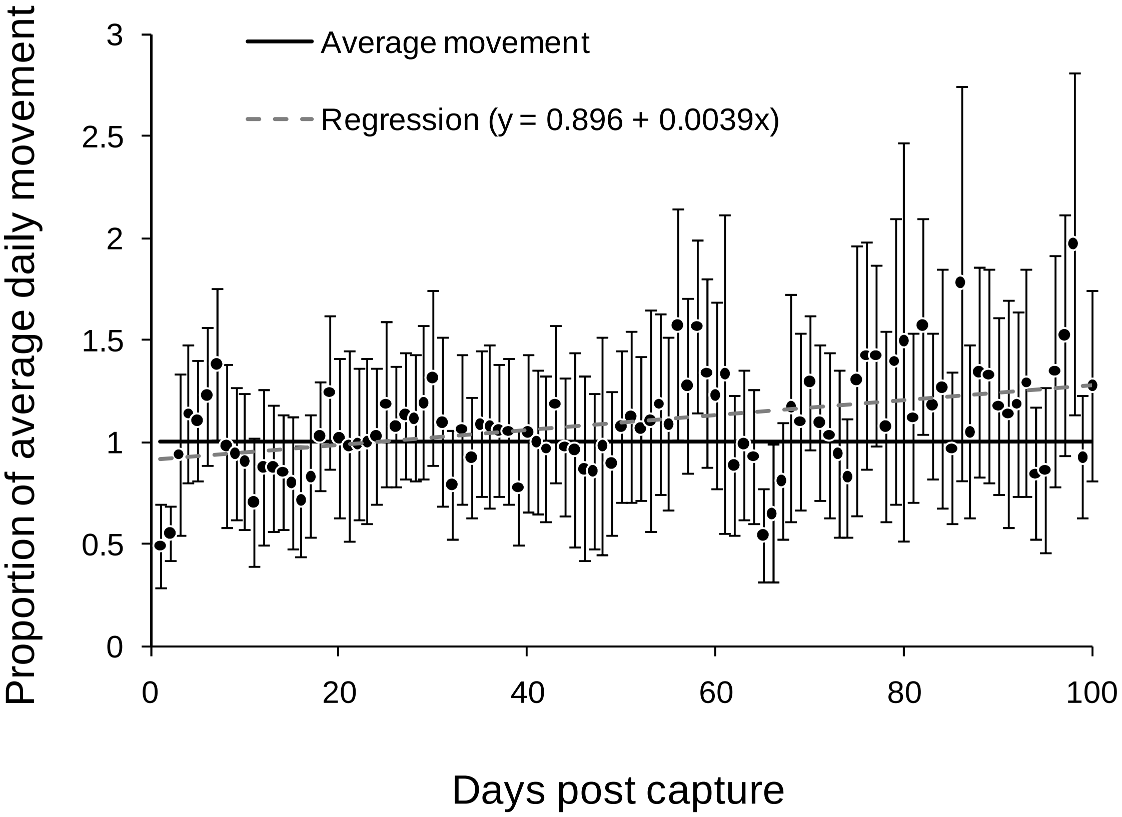

Figure II.2: The mean and 95% CI of the daily proportion of average movement between 1 and 100 days post-capture of 3,208 daily observations for 36 cougars collared with Lotek 4400S GPS collars that did not succumb to starvation in west central Alberta. Also displayed is the regression through all 3,208 observations, which possesses a statistically significant positive slope (P = <0.001), but explains little of the total variation in movement ($R^2 = 0.008$).

Table II.1: A comparison of first 51 day and post-51 day kill rates (kg/day) after capture (day 0) for each cougar age-sex class and all cougars that were continuously monitored for ≥70 days in west central Alberta, Canada.

Cougar age-sex	Mean proportion of post-51-day kill rate observed in the first 51 days	n	Paired t-test (p-value)
Family Group	1.03	10	0.370
Adult Female	1.10	7	0.454
Adult Male	1.13	5	0.174
Sub-adult Male	0.89	6	0.217
Sub-adult Female	0.76	7	0.213
All Cougars	1.02	35	0.440

DISSCUSSION

Cougars that did not succumb to starvation failed to exhibit any long-term negative effects of capture and collaring. The short-term (2-day) depression of movement I detected immediately after capture and anesthesia was not unexpected. Logan et al. (1999) reported a similar brief depression of movement for cougars captured in leghold snares in New Mexico. The tendency toward lower kill rates in the first 51 days post-capture in sub-adults, is most likely a result of improved predatory efficiency with increasing age (Chapter 4) and not a result of capture effects. The fact that I could not discern long-term capture effects that resolved themselves during the timeframe of my analyses, however, is not sufficient to prove that no long-term effects were present. It remains possible that collaring cougars causes permanent behavioral changes similar to those that have been reported for Zebra wearing heavier radiocollars in Africa (Brooks et al. 2008).

I had the unusual opportunity to assess the hunting behavior of uncollared cougars, however, in two cases where I was able to monitor kill rates via collared offspring (the case of 9898R discussed above and a similar case where the adult female was never collared). Kill rates I calculated for these animals (9.5 and 11.7 kg/day) were very similar to the average I recorded for eight GPS collared females with kittens > 6 months old (11.8 kg/day, SD = 1.01). This suggests that collaring may not have a large effect on the predatory behavior of cougars that do not quickly succumb to starvation. Data on the hunting behavior of unmarked cougars are difficult to obtain, and although the sample size is insufficient for large scale inference, the results from these 2 case studies are encouraging.

For cougars that starved to death (7% of captures during this study), on the other hand, the effect of collaring was severe. In each case delayed capture related mortality is a much more parsimonious explanation than starvation due to natural causes. First, cougar body condition deteriorated rapidly from a healthy state at capture, suggesting a link between capture and mortality. Second, although the sample size is small (n = 1), 9898R demonstrated a dramatic decline in predatory behavior associated directly with the capture event, strongly implicating capture as the cause of this behavioral change. Although cougar mortalities have been reported as an immediate consequence of capture in other studies (Hornocker 1970, Anderson et al. 1992, Logan et al. 1999, Lambert et al. 2006), I am unaware of any previous reports of delayed capture-related mortality in this species.

Frustratingly, I was unable to ascertain a specific set of circumstances (related to the particulars of the capture or to individual animals) that made cougars that succumbed to starvation different from those that survived. The primary identifiable commonality among cougars that died of post-capture starvation was that they were adult females with kittens. However, I captured 10 other individuals of this same age-sex and reproductive status that survived. Indeed, in several cases, cougars that I expected might have an increased propensity to starvation because of their physical circumstances at capture (e.g., poor body condition, large abscesses and heavy infection caused by rotting teeth, missing teeth/claws, blindness in one eye, etc.) survived without incident.

I used Telazol as the primary immobilizing agent during cougar captures. Some reports of the use of Telazol in tigers (*Panthera tigris*) suggest that this drug may have negative side effects (Armstrong 1990, Vogelnest 1999), and one recent popular media article blames Telazol for the delayed post-capture mortality of 2 tigers in the Sundarban forest, Bangladesh (Hossain 2008). The possibility that Telazol would have negative effects on felids in general has also been raised (Hossain 2008). However, a recent review of the literature suggests that there is little evidence to support the claim that Telazol is contraindicated for tiger immobilization (T. J. Kreeger, Wyoming Game and Fish Department, personal communication), and despite its common use (e.g., Anderson and Lindzey 2003, Mattson 2007) no deaths due to anesthetic complications related to Telazol have previously been reported for cougars. I found no evidence to suggest that Telazol might have contributed to the cougar mortalities reported here. Indeed, the complications that have been reported for tigers involve rear-limb ataxia (Armstrong 1990), which would restrict movement. The cougars that succumbed to starvation in west-central Alberta remained highly mobile.

Stress is also known to be a factor capable of causing anorexia in animals (Marti et al. 1994). Because capture and collaring are inherently stressful experiences for wild animals, stress cannot be ruled out as an aggravating cause of death in the 4 cases of capture-related mortality presented here. Stress and injury at capture can be reduced by selecting appropriate capture techniques when attempting to collar large carnivores (Frame and Meier 2007, Cattet et al. 2008a). For cougars this might mean limiting chase duration, using discretion when darting (e.g., selecting suitable trees for the safety of both animals and researchers), and choosing appropriate remote injection tools set to the correct propulsion power. However, it is impossible to eliminate all stress associated with the capture of a wild animal, and if the collar itself represents a significant source of stress, then the stressor remains present even after the capture procedure has been completed. Lighter, smaller collars may alleviate some of these effects (Brooks et al. 2008), and researchers and collar manufacturers should strive to improve technology accordingly. Even if some form of capture or collar related stress was the driving force behind the starvation mortalities observed during my study, however, the question of why it affected some cougars but not others remains unanswered.

Although I am unable to provide more than general suggestions for preventing future occurrences of delayed capture related mortality in cougars, my findings do have important implications for the analysis and interpretation of research results. Predation and survival data from cougars dying as a result of capture and collaring, for instance, should be excluded from population level analyses to avoid erroneous inference. Wildlife biologists should remain cognizant of the possibility of delayed capture related mortality and carefully evaluate the causes of apparently natural mortalities (e.g., starvation), even if they take place >30 days post-capture. Importantly, however, the negative effects associated with collaring cougars in my study appeared to be an all-or-none response. In contrast to the findings of Cattet et al. (2008) with respect to black and grizzly bears, therefore, my results do not support truncating or omitting data when estimating predation, movement, or survival parameters from cougars that did not suffer delayed capture-related mortality. Future research should continue to test the robustness of these conclusions.

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APPENDIX III

GPS COLLAR FAILURE CAUSED BY CANINE PUNCTURE OF BATTERY CASES FOR UNITS DEPLOYED ON MALE COUGARS IN ALBERTA

Store-on-board and remotely downloadable Global Positioning System (GPS) telemetry devises are increasingly important tools used to study a variety of aspects of animal ecology (Rodgers et al. 1996, Hurlbert and French 2001, Anderson and Lindzey 2003, Nielsen et al. 2003). Their use has been especially prevalent for larger mammals such as ungulates and large carnivores, but technology is advancing quickly and GPS telemetry has seen a much broader application in recent years (e.g., Vyssotski et al. 2006). GPS telemetry provides substantial advantages over older radiotelemetry technology, primarily because of increased efficiency and accuracy: GPS telemetry units record the precise location of an animal at regular intervals (often multiple times per day) even when researchers are not in the field. Researchers studying cougar (*Puma concolor*) ecology have been using GPS telemetry collars for nearly a decade (Anderson and Lindzey 2003), and their use in research projects begun after 2005 is almost ubiquitous (Toweill et al. 2008). The detail and precision of GPS telemetry has permitted cougar researchers to make rapid advances concerning several aspects of cougar behavior, ecology and conservation, especially with respect to cougar foraging ecology (e.g., Anderson and Lindzey 2003, Chapter 3, Chapter 4, Chapter 5).

However, GPS telemetry collars are not without their downsides. First, they are expensive and projects hoping to deploy them must secure substantial funding. Second, they are notorious for failing to meet expectations (Johnson et al. 2002, Gau et al. 2004, Hebblewhite et al. 2007). Entire research projects and, in many cases, conservation programs hinge on GPS collar technology functioning properly, and GPS collar failures can be devastating. Consequently, it is critical that information about failure rates and the cause of failure (if it is known) are shared among researchers in order to improve the prospect of success in future studies. In this appendix, I report on GPS collar failure rates in units deployed on cougars for research purposes in west-central Alberta and in the

Cypress Hills Provincial Park, Alberta, Canada, during 2005-2009. Additional information about the objectives and preliminary results of the Cypress Hills cougar study can be found in Bacon and Boyce (2009) and Bacon et al. (2009).

The primary data collection tool used in both west-central Alberta and in the Cypress Hills was the Lotek 4400S GPS collar equipped with remote download capabilities. The collars also gave off a standard very high frequency (VHF) radio pulse (Lotek Engineering, Newmarket, Ontario, Canada, http://www.lotek.com/gps4400.htm). Lotek 4400s units were deployed at 48 captures (16 on males, 32 on females). The same cougar was occasionally collared more than once, and my sample of different individuals collared with Lotek 4400S units included 15 males and 28 females. All collars were programmed with a GPS fix interval of 3 hours and battery life was expected to last for approximately 14 months. Most collars were programmed to drop off after 12 months to ensure plenty of time for retrieval while the batteries were still functioning. GPS data were downloaded from each collar once every 2-weeks and attempts were made to locate each collared animal at least once/week using traditional VHF telemetry. In addition, in west-central Alberta, I deployed H.A.B.I.T VHF/GPS collars (H.A.B.I.T research, Victoria, British Columbia, Canada) at 6 captures.

All 6 H.A.B.I.T collars (100%) experienced complete GPS failure due to poor design of the GPS antenna. The company has since gone out of business. I had better success with Lotek 4400s collars, but failure was still common and I recorded 14 cases of complete GPS malfunction before 1 year of data collection had been achieved (29% of all collars deployed). In 12 of those cases, collar failure was catastrophic and both VHF and GPS components were lost, while in 2 other cases only the GPS component stopped working. Failure rates of collars deployed on males (10 of 16, or 63%) were much higher than those deployed on females (4 of 33, or 12.5%). Because of the value of the GPS collars, substantial effort was invested into retrieving lost units. In west-central Alberta, collar retrieval was accomplished through intensive recapture efforts on four occasions, and in one exceptional case in the Cypress Hills the failed collar was found still attached to a cougar that had been killed during a botched attempt to take down an elk. Six failed collars were also returned in west-central Alberta after the cougars wearing them were harvested by licensed hunters.

Consequently, in 11 cases (3 for females and 8 for males) I was able diagnose the cause of collar failure, while in 3 cases (1 for females and 2 for males) cause of failure remains unknown. Collars deployed on female cougars failed because of manufacturers defects relating to power draw on the battery (n = 2) or improper sealing which led to water damage (n = 1). All collars worn by males that were recovered, on the other hand, failed due to canine tooth punctures that perforated the battery case (n=8, Figure III.1). In one case, a portion of the tooth of the cougar that had bitten through the collar was broken off and remained inside the battery case where it was located when the collar was recovered. Whether the punctures were made during fights between males or during mating associations with females remains uncertain. In most cases, however, I strongly suspect the latter explanation because when the collars were recovered they were badly damaged by repetitive chewing (e.g., Figure III.1), yet the male cougars themselves (which I observed at re-capture or in photos and descriptions provided by hunters) were otherwise unscathed (i.e., lacking scars or other obvious physical damage).

As a consequence of these findings, I strongly urge collar manufacturers and cougar researchers who plan to develop or purchase GPS telemetry collars for use on cougars in future studies to consider the durability of the material used to encase the battery and electronics, especially for units that are intended for deployment on male cougars. If collar biting by cougars is as common in other places as it is in Alberta (either as a result of mating associations or fights among males) then instrumenting male cougars with GPS collars built with softer plastics that can easily be perforated by the bite of another cougar (such as those used for the Lotek 4400S units during my study and in the Cypress Hills) may result in collar failure, loss of GPS units, loss of data, and perhaps even harm to cougars (e.g., the observation of a broken tooth found in the battery casing).

Figure III.1. A Lotek 4400S collar worn by an adult male cougar in the Cypress Hills, Alberta, Canada during 2007-2008 and subjected to substantial damage and perforation of the battery pack due to biting/chewing by another cougar (photo courtesy of Michelle Bacon).

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APPENDIX IV

AGE, SEX, MONITORING PERIOD, AND FATE OF COUGARS CAPTURED AND RADIOCOLLARED FOR RESEARCH PURPOSES IN WEST-CENTRAL ALBERTA DURING 2005-2008

I radiocollared 44 cougars in the Clearwater County of west-central Alberta between 1 December 2005 and 30 March 2008. At capture, my sample of cougars consisted of 22 adult females (50%), 6 adult males (14%), 7 sub-adult females (16%), and 9 sub-adult males (20%). Two subadult males and three subadult females transitioned to adults over the course of my study. I monitored cougars for a total of 12,080 radio-days, averaging 275 days per cougar with a range of 24 – 677 days (Table IV.1). The fate of 18 marked cougars was unknown because collars were removed or failed or because cougars were not relocated after active radiotelemetry monitoring ended in August 2008. In 16 cases, the fate of marked cougars was known because cougars died while they were actively monitored with radiotelemetry. In 10 additional cases fate was identified after collars were removed or failed because individuals with unique ear tag numbers were registered at an Alberta Fish and Wildlife office after being killed by hunters or found dead (Table IV.1).

Sources of Mortality

Of cases where fate was known, 15 animals were killed by licensed hunters, 1 was legally killed by a landowner, 1 was poached by a hunter in a closed zone, 4 were snared accidentally, 1 died of natural causes after falling from a tree, and 4 died as a result of delayed effects of capture and collaring (Appendix II). These data update those presented in Chapter 3 and in Appendix II by incorporating known hunting mortalities during winter 2008/2009 and one natural mortality in January 2010. The additional mortality data support my earlier finding that males were particularly prone to harvest by hunters (Chapter 3). Indeed, few males in the Clearwater County died by other means and 80%

of male cougars captured and marked during my study were shot by licensed hunters or poached before the end of the 2008/2009 hunting season (Table IV.1).

Natural mortalities did occasionally occur in the cougar population, and I located 3 instances of cannibalism at the GPS location clusters of collared cougars. The first incident involved a ~7 month old kitten that was killed by a collared adult male, the second an adult female killed by a collared adult male, and the third a dispersal-age male that was either killed or scavenged by a collared adult female. A fourth uncollared cougar was found dead of apparent malnutrition during the course of my study, and a fifth cougar that I helped capture in the town of Nordegg after it attempted to kill a dog was put down due to severe malnutrition.

Nevertheless, only one cougar in my marked sample (3.8%) died of natural causes (Table IV.I). This adult female climbed a tree and apparently fell, wedging herself between the trunk of the tree she climbed and an adjacent tree (Figure IV.1). During snowtracking sessions conducted during my study (>1,100 km), cougars were never observed climbing trees except when pressured by hounds, wolves, or people. Thus tree climbing appears to be used almost exclusively to escape danger, but it is also a strategy that may occasionally prove hazardous (Figure IV.I). In addition to the case of a climbing mortality presented here, at least two instances of cougars electrocuting themselves after climbing power poles have been reported (Logan and Sweanor 2001, Thompson and Jenks 2009).

Figure IV.1: An adult female cougar (9893R) found dead after falling and wedging herself between the trunks of two trees. Fish and Wildlife officers responding to the incident were unable to determine what caused the cougar to climb the tree in the first place (Photo courtesy of Lori Backen, Alberta Fish and Wildlife).

On Compensatory Mortality in Hunted Cougar Populations

Sustainable harvests of wildlife populations are predicated on the idea of compensation for harvest mortality. Compensation is the demographic response of a population to mortality, and is attributed to density dependence (Boyce et al. 1999). This means that where compensation occurs, reductions in population size will result in density-dependent increases in birth rates, survival, or immigration, making sustainable harvests possible (Czetwertynski et al. 2007). A key prediction of the demographic response of a harvested population where compensation occurs is "a decrease in natural mortality in response to the reduction in population size caused by predation or harvest" (Boyce et al. 1999 pg. 420).

Recently, a debate has begun over whether or not cougar populations are capable of compensating for harvest mortality. Based on new experimental evidence from Washington State, Cooley et al. (2009) have asserted that human-caused mortality is additive to other mortality sources in cougar populations. In contrast, Quigley and Hornocker (2009, pg. 66) contend that cougar populations experience a "compensatory mechanism in which human-caused mortality is replacing natural mortality in human-impacted ecosystems". This view is consistent with a number of studies that found low rates of natural mortality in hunted cougar populations (Ross and Jalkotzy 1992, Anderson and Lindzey 2005, Lambert et al. 2006), and contrast with higher rates of natural mortality found in unhunted populations (Hemker et al. 1984, Beier and Barrett 1993, Logan and Sweanor 2001). The mortality patterns identified during my study in west-central Alberta appear to provide additional support for Quigley and Hornocker's interpretation of the data in that harvest mortality was high and natural mortality almost non-existent.

The distinction between the additive mortality hypothesis expressed by Cooley et al. (2009) and the compensatory or partially compensatory hypothesis advocated by Quigley and Hornocker (2009) is critical for effective management of hunted cougar populations (Williams et al. 2002). If human-caused mortality is entirely additive, achieving sustainable harvest of cougar populations will be difficult, especially where natural mortality is already high. If this is true, managers must be substantially more conservative when allocating cougar harvest than if there is a certain amount of compensation for harvest mortalities. Unfortunately, much of the data available for cougars do not allow for rigorous testing of the compensatory mortality hypothesis, only preliminary assessment of the prediction presented by Boyce et al. (1999) that natural mortality rates should be lower. Indeed, the compensatory mortality hypothesis has proven notoriously difficult to test rigorously for a variety of species (e.g., Sedinger et al. 2010).

Cooley et al. (2009) made the first attempt to provide experimental evidence capable of testing the prediction that natural mortality decreases in hunted cougar populations; as such their findings deserve careful scrutiny. Cooley et al. (2009) contrasted 2 cougar populations in Washington, USA, one of which was exposed to heavy hunting while the other was lightly hunted. They rejected the hypothesis that hunting mortality can be compensatory in cougars because they found high natural mortality in the heavily hunted population, reproduction rates did not change between populations, and, in direct contrast with the predictions of the compensatory mortality hypothesis, kitten survival was lower in the heavily hunted population. However, as noted above compensation in the form of reduced mortality from natural causes and increased kitten production is thought to be density-dependent (Caughley and Sinclair 1994, White and Bartmann 1998). Hence compensation should not be expected unless the population is reduced (Boyce et al. 1999).

In the Washington case, cougar density in the heavily hunted population was equal to that in the lightly hunted population, and the size of the heavily hunted population did not change over the course of the study. The population was maintained by immigration, possibly because heavy harvest occurred over a spatial extent too small relative to cougar dispersal distance to achieve density reduction (Robinson et al. 2008). Cooley et al.'s (2009) rejection of the compensatory mortality hypothesis may therefore be premature. Indeed, the higher rates of immigration in the heavily hunted population can be considered a form of compensation for hunting mortality, highlighting the potential complexity of the compensatory mortality hypothesis. Additional experimental research where carrying capacity remains constant and vital rates are measured in response to changing cougar density is needed to continue to address this important issue.

Cooley et al. (2009) do bring up an important point, however, when they suggest that higher kitten mortality in their heavily hunted population might be related to increased sexually selected infanticide by males. Sexually selected infanticide is a common rationalization for infant killing by males in both carnivores and primates (Hrdy 1974, Packer and Pusey 1983, Knopff et al. 2004), and several studies provide circumstantial evidence for it in cougars (Ross and Jalkotzy 1992, Logan and Sweanor 2001). Sexually selected infanticide could dampen compensatory effects in cougars, but it also remains an untested hypothesis and more research is needed to clarify its prevalence in cougar populations and its influence on population dynamics.

Until additional information on compensation and sexually selected infanticide become available, it is important for Alberta's cougar managers to recall that cougar harvests have apparently been sustainable over the past several decades and that despite high harvest, the cougar populations appear to be growing (Appendix I).

Table IV.1: Age, sex, monitoring period and fate of cougars captured and radiocollared for research purposes in west-central Alberta during 2005-2008.

Cougar Characteristics			**Monitoring**			**Fate**		
ID (ear tag)	Age at Capture	Sex	Start	End	Radio-days	Mortality Status	Mortality Month and Year	Comments
0003R	Sub-Adult	Female	1-Dec-05	28-Feb-07	455	Unknown	–	Lost contact with collar prematurely. Failure? Dispersal? Poaching?
0108R	Sub-Adult	Female	7-Jan-08	24-Jul-08	200	Unknown	–	Monitoring ended
0109R	Adult	Female	22-Jan-08	9-Mar-08	48	Capture/Collar Mortality	March 2008	Delayed capture related mortality
0110R	Sub-Adult	Female	27-Jan-08	5-Aug-08	192	Unknown	–	Monitoring ended
0111R	Sub-Adult	Male	5-Mar-08	5-Aug-08	154	Hunter Harvest	January 2009	Harvested after radiotelemetry monitoring ended
0112R	Adult	Female	6-Mar-08	9-Aug-08	157	Unknown	–	Monitoring ended
0113R	Sub-Adult	Male	16-Mar-08	29-Jul-08	136	Hunter harvest	December 2008	Harvested after radiotelemetry monitoring ended

0114R	Sub-Adult	Male	25-Mar-08	29-Jul-08	127	Hunter harvest	December 2008	Harvested after radiotelemetry monitoring ended
0115R	Adult	Female	30-Mar-08	23-Jul-08	116	Hunter harvest	January 2009	Harvested after radiotelemetry monitoring ended
9822R	Adult	Female	13-Dec-05	21-Feb-06	71	Accidental Snaring	February 2006	Collar retrieved
9823R	Sub-Adult	Female	11-Jan-06	15-Jun-07	521	Unknown	–	Collar failure
9824R	Sub-Adult	Male	20-Jan-06	16-Dec-06	331	Hunter harvest	December 2006	Collar retrieved
9825R	Adult	Female	22-Jan-06	8-Dec-06	321	Hunter harvest	December 2006	Collar retrieved
9827R	Adult	Male	18-Feb-06	14-Jan-07	331	Hunter harvest	January 2007	Collar retrieved
9828R	Sub-Adult	Female	4-Dec-06	15-Jul-08	590	Unknown	–	Monitoring ended
9829R	Adult	Male	18-Feb-06	26-Dec-07	677	Accidental Snaring	December 2007	Collar retrieved
9830R	Adult	Female	20-Feb-06	9-Apr-06	49	Capture/Collar Mortality	April 2006	Delayed capture related mortality
9871R	Adult	Female	21-Feb-06	16-Jun-07	481	Unknown	–	Collar failure

9872R	Adult	Male	18-Feb-06	13-Mar-06	24	Unknown	–	Suspected collar failure. However, 9872R used rural farming landscapes extensively. Possible poaching?
9873R	Adult	Female	28-Feb-06	9-Dec-07	650	Unknown	–	Collar retrieved
9874R	Adult	Female	1-Mar-06	20-Apr-06	51	Capture/Collar Mortality	April 2006	Delayed capture related mortality
9875R	Adult	Female	8-Dec-07	25-Feb-08	80	Accidental Snaring	February 2008	Collar retrieved
9876R	Adult	Male	12-Mar-06	23-Feb-07	349	Poaching	February 2007	Illegal harvest after quota was already filled
9877R	Sub-Adult	Male	17-Dec-07	15-Jul-08	212	Hunter harvest	January 2009	Harvested after radiotelemetry monitoring ended
9878R	Adult	Female	15-Mar-06	19-Mar-07	370	Unknown	–	Collar retrieved
9879R	Adult	Female	24-Mar-06	12-Feb-07	326	Unknown	–	Collar retrieved
9881R	Sub-Adult	Male	17-Dec-06	8-Mar-08	448	Hunter harvest	January 2009	Harvested after radiotelemetry monitoring ended

9883R	Adult	Female	13-Jan-07	15-Jul-07	184	Unknown	–	Collar failure
9884R	Adult	Female	10-Feb-07	16-Dec-07	310	Hunter harvest	December 2007	Collar retrieved
9885R	Sub-Adult	Female	14-Dec-07	25-Jul-08	225	Unknown	–	Monitoring ended
9886R	Sub-Adult	Female	16-Mar-07	2-Feb-08	324	Hunter harvest	February 2008	Collar retrieved
9887R	Sub-Adult	Male	18-Mar-07	16-Apr-08	396	Hunter harvest	January 2009	Harvested after radiotelemetry monitoring ended
9888R	Adult	Female	6-Apr-07	4-Feb-08	305	Accidental Snaring	February 2008	Collar retrieved
9889R	Adult	Male	5-Apr-07	15-Jun-08	438	Hunter harvest	December 2008	Harvested after radiotelemetry monitoring ended
9890R	Adult	Female	6-Apr-07	6-Apr-08	367	Unknown	–	Collar retrieved
9891R	Adult	Female	10-Feb-07	13-Oct-07	246	Unknown	–	Collar retrieved
9892R	Adult	Female	8-Mar-07	25-Mar-08	384	Unknown	–	Collar ran out of battery (failed to blow off)
9893R	Adult	Female	20-Jan-07	6-Dec-07	321	Natural mortality	January 2010	Found dead after falling from a tree and becoming stuck (Figure IV.1)

9894R	Adult	Female	7-Apr-07	24-Feb-08	324	Landowner kill	February 2008	Shot by landowner after killing llama
9895R	Sub-Adult	Male	7-Nov-07	19-Jan-08	74	Hunter harvest	January 2008	Collar retrieved
9896R	Adult	Female	6-Dec-07	23-Jul-08	231	Unknown	–	Monitoring ended
9897R	Adult	Male	6-Apr-07	1-May-08	392	Unknown	–	Collar ran out of battery (failed to blow off)
9898R	Adult	Female	4-Feb-07	28-Feb-07	25	Capture/Collar Mortality	February 2007	Delayed capture related mortality
9899R	Sub-Adult	Male	20-Mar-07	25-May-07	67	Hunter harvest	December 2008	Harvested after radiotelemetry monitoring ended.

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APPENDIX V

HOME RANGE CHARACTERISTICS AND DISPERSAL OF GPS COLLARED COUGARS IN WEST-CENTRAL ALBERTA DURING 2005-2008

For this appendix, I mapped the location of cougar home ranges within my study area for each animal captured and collared with a Global Positioning System (GPS) telemetry collar. Next, I summarized monitoring duration, number of GPS locations, fix success, and home range characteristics for each cougar. Finally, I analyzed available information on the dispersal behavior of subadults. Data were derived from 43 GPS collared cougars (individuals were instrumented either a Lotek 4400S GPS collar, a H.A.B.I.T GPS/VHF collar, or wore both at different times) during 2005-2008.

Spatial Distribution of Collared Cougars in the Study Area

I selected a large study area in order to encompass variation in the combination of density and relative abundance of prey necessary to investigate prey switching and functional response in cougars (Chapter 5). Consequently, I made a concerted effort to capture cougars from across my study area, with considerable success (Figures V.1-V.3). However, I collared fewer animals in the rugged mountains bordering Jasper and Banff National Parks where access was limited than I did in the eastern two thirds of the study area where road and trail access was high. Although I attempted to avoid capturing dependent kittens, I otherwise captured cougars as encountered. I instrumented twice as many females (*n* = 29) as males (*n* = 14) with GPS collars, which presumably reflects the greater relative abundance of females in the cougar population (Appendix I).

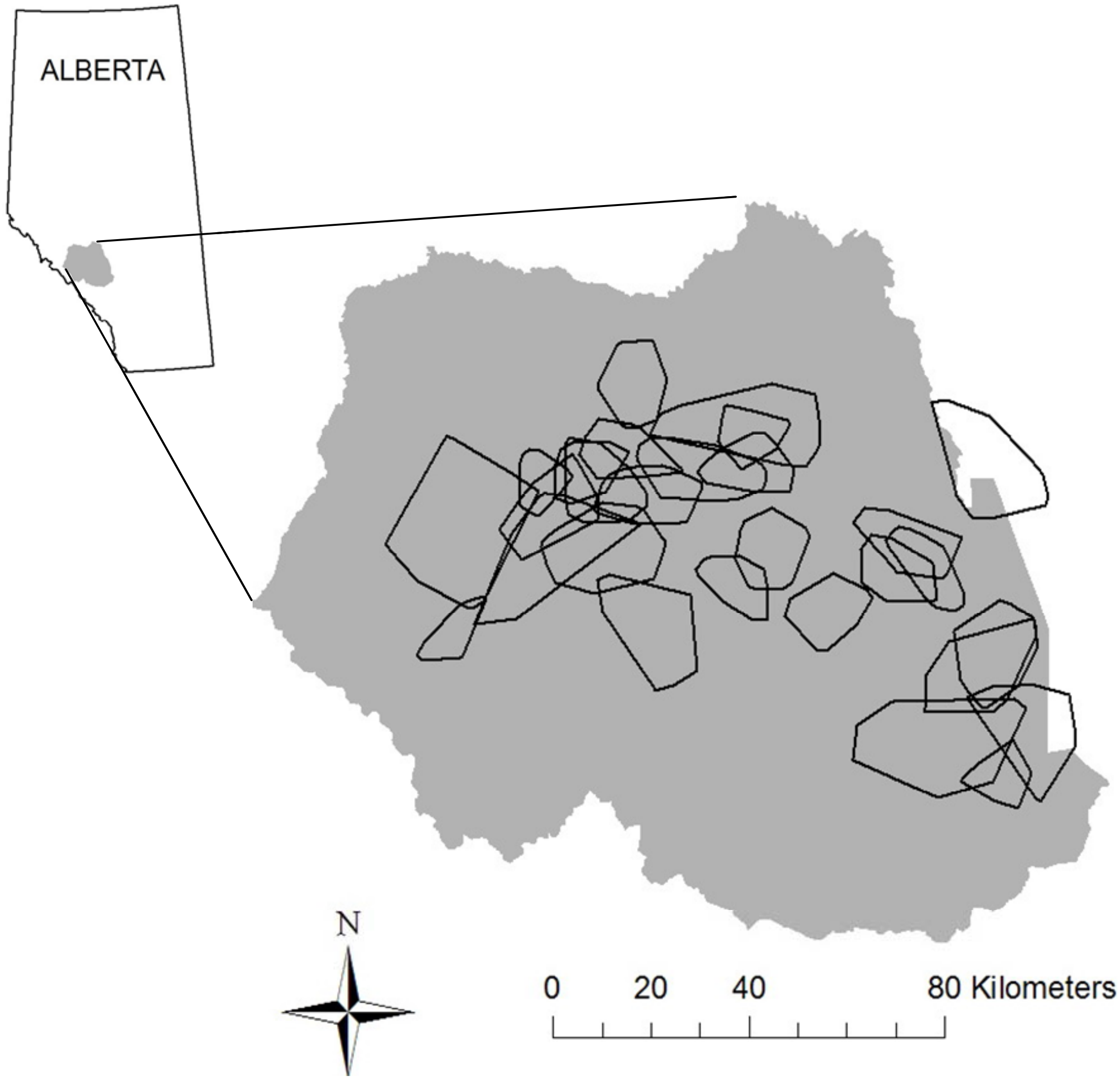

Figure V.1: Minimum convex polygon home ranges (100%) of all GPS locations for each female cougar captured and collared with a GPS radiocollar as part of the Central East Slopes Cougar Study in west-central Alberta, Canada during 2005-2008.

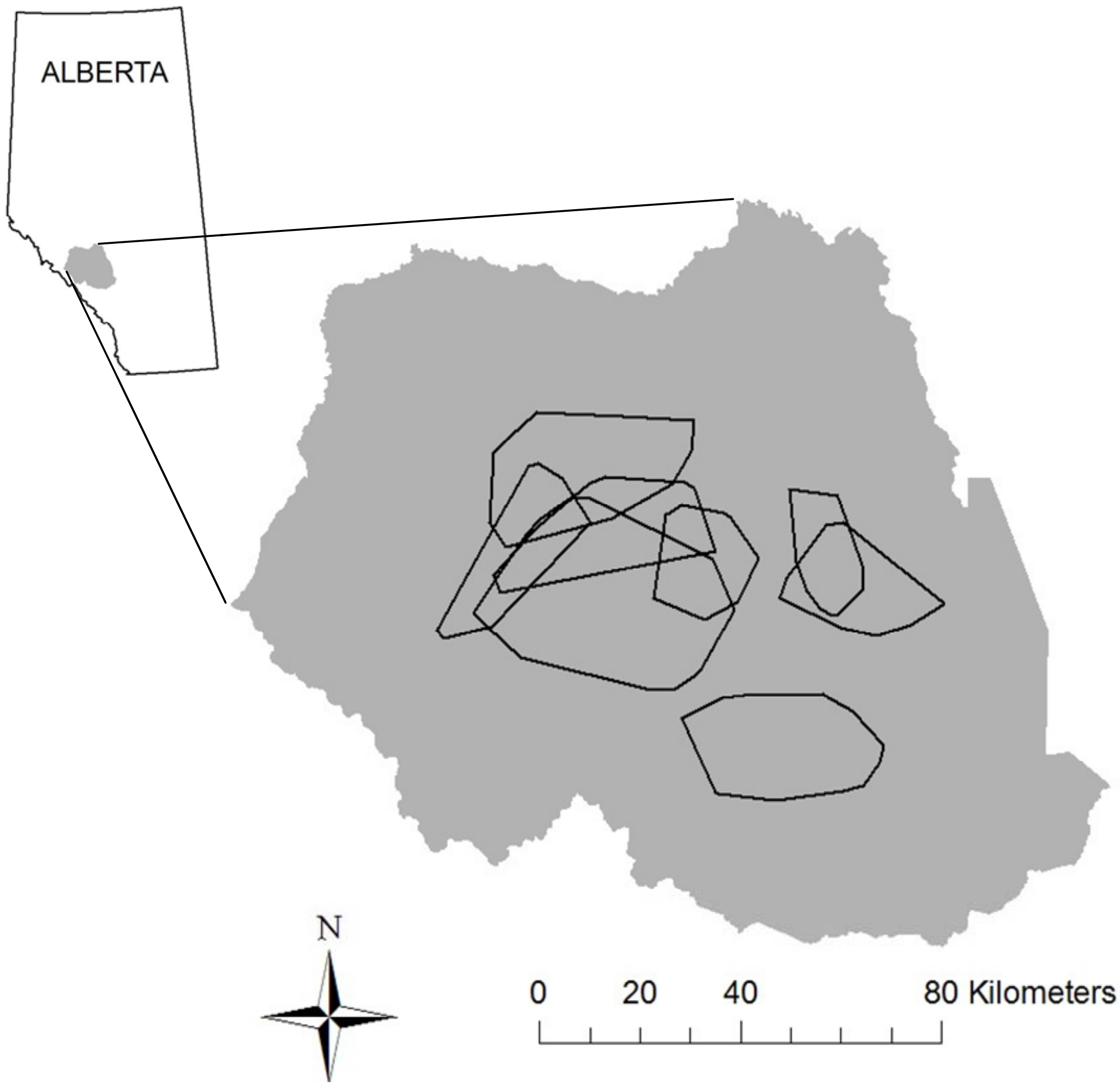

Figure V.2: Minimum convex polygon home ranges (100%) of all GPS locations for each resident adult male cougar captured and collared with a GPS radiocollar as part of the Central East Slopes Cougar Study in west-central Alberta, Canada during 2005-2008. Also included are the home ranges of 2 males aged as sub-adults at capture that maintained stable home ranges.

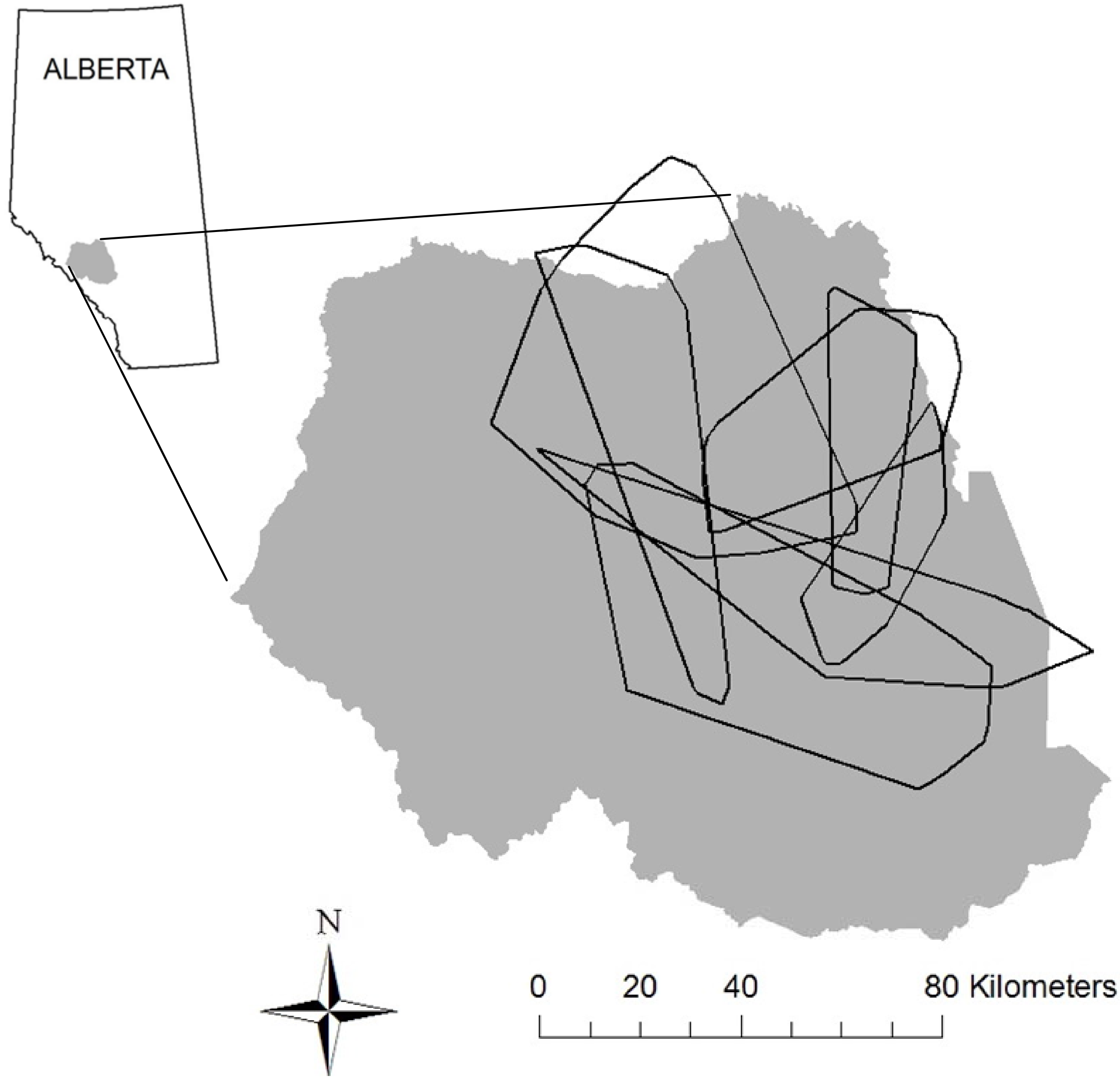

Figure V.3: Minimum convex polygon home ranges (100%) of all GPS locations for each dispersing sub-adult male cougar captured and collared with a GPS radiocollar as part of the Central East Slopes Cougar Study in west-central Alberta, Canada during 2005-2008.

Home Range Characteristics

I calculated 95% and 100% minimum convex polygons using all location data obtained for each cougar (Table V.1). An analysis of growth in home range size as a function of monitoring time indicated that cougars use >50% of their annual 100% MCP home range in the first 10 weeks of monitoring and >80% by 26 weeks. Average annual 100% MCP home range size for 13 resident adult females monitored at least 28 weeks (not including data beyond the first 52 weeks) was 208 km^2 (SD = 85) and the average 100% MCP home range of 4 males monitored over similar duration was 769 km^2 (SD = 406).

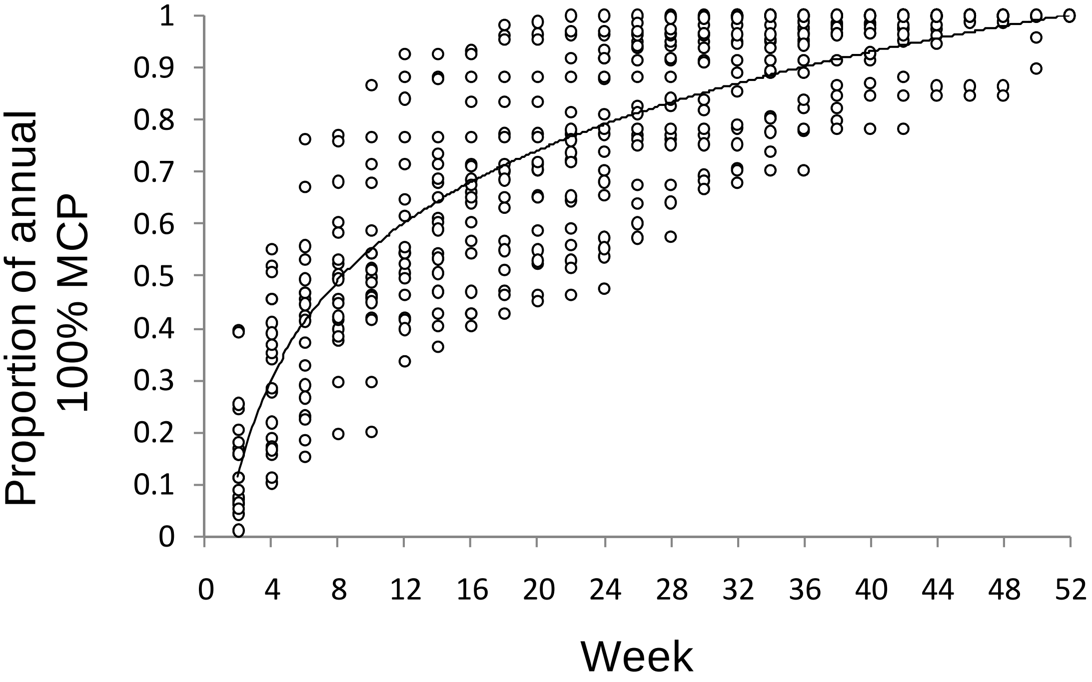

Figure V.4: Proportion of annual 100% minimum convex polygon (MCP) home range given by the 100% MCP calculated using cumulative location data at 2-week intervals for 15 cougars monitored at least 42 weeks in west-central Alberta during 2005-2008. The best logarithmic fit to the data is displayed.

Dispersal

Only one cougar (9899R) dispersed out of the study area entirely. This sub-adult male traveled 148 straight line kilometers between his capture location near Caroline in March 2007 and the location where he was shot by a licensed hunter near Cynthia in December 2008. Dispersal by sub-adult males out of the study area may have been limited by the large size of the study area and the fact that much of the Clearwater County was probably a cougar population sink during 2005-2008, especially for the heavily harvested males (Chapter 3, Appendix IV). Consequently, males might not have needed to disperse great distances to find an available home range. Most individuals (7 of 9) assigned to the sub-adult male age class at capture, however, demonstrated unstable home range characteristics consistent with dispersal. Dispersing sub-adult males ranged over vast areas while they were monitored (i.e., up to 3,502 km^2, Figure V.3), which is consistent with the hypothesis that male cougars are obligate dispersers and rarely maintain home ranges overlapping their natal range (Logan and Sweanor 2001). Four of seven dispersing males were shot by licensed hunters before they established a stable home range, but 3 other animals became resident within a sub-portion of their dispersal range inside the study area. Of the 7 animals assigned to the sub-adult female category at capture, only one exhibited a home range shift, moving approximately one female home range over 3 months post-capture. All other sub-adult females maintained consistent home ranges from the time of initial capture. Whether this is because they did not disperse or because they dispersed prior to capture is unknown.

Table V.1: GPS monitoring periods, collar fix success, and home range characteristics of cougars in west-central Alberta during 2005-2008.

Cougar Characteristics				**GPS Monitoring**					**Range (km^2)**	
				Lotek 4400S			H.A.B.I.T. GPS			
ID (ear tag)	Age at Capture	Sex	Dispersing	GPS Days	Number of Fixes	Fix Success	Number of Fixes	Fix Success	100% MCP	95% MCP
0003R	Sub-Adult	F	No	336	1213	45.26%	-	-	304	175
0108R	Sub-Adult	F	No	200	1436	90.26%	-	-	382	243
0109R	Adult	F	No	48	269	71.35%	-	-	89	81
0110R	Sub-Adult	F	?	192	911	59.62%	-	-	620	477
0111R	Sub-Adult	M	Yes	154	682	55.90%	-	-	1387	1218
0112R	Adult	F	No	157	704	69.22%	-	-	160	147
0113R	Sub-Adult	M	No	136	945	87.66%	-	-	255	170
0114R	Sub-Adult	M	Yes	127	900	89.46%	-	-	703	649
0115R	Adult	F	No	116	558	60.72%	-	-	238	228

9822R	Adult	F	No	71	298	53.02%	-	-	180	165
9823R	Sub-Adult	F	?	454	1535	54.05%	302	38.52%	512	468
9824R	Sub-Adult	M	Yes	164	879	67.93%	-	-	836	777
9825R	Adult	F	No	321	1446	57.36%	-	-	185	141
9827R	Adult	M	No	290	1141	49.31%	-	-	773	599
9828R	Adult	F	No	626	1372	79.86%	133	46.18%	211	177
9829R	Adult	M	No	73	347	60.56%	-	-	599	503
9830R	Adult	F	No	49	241	62.60%	-	-	301	278
9871R	Adult	F	No	390	1747	63.07%	146	42.44%	333	306
9872R	Adult	M	No	24	146	80.66%	-	-	418	415
9873R	Adult	F	No	650	3331	64.21%	-	-	204	179
9874R	Adult	F	No	51	293	73.07%	-	-	96	64
9875R	Adult	F	No	80	562	89.06%	-	-	119	98

9876R	Adult	M	No	349	1462	52.53%	-	-	657	569
9877R	Sub-Adult	M	Yes	212	1218	72.11%	-	-	3502	3431
9878R	Adult	F	No	342	1655	62.57%	0	0.00%	252	233
9879R	Adult	F	No	326	1640	63.10%	-	-	250	194
9881R	Sub-Adult	M	Yes	144	1004	87.92%	-	-	452	276
9883R	Adult	F	No	74	-	-	222	37.50%	109	109
9884R	Adult	F	No	309	1440	67.67%	-	-	155	116
9885R	Sub-Adult	F	No	226	1659	92.58%	-	-	339	234
9886R	Sub-Adult	F	No	324	1964	75.95%	-	-	287	236
9887R	Sub-Adult	M	Yes	396	1972	69.90%	-	-	2890	2847
9888R	Adult	F	No	305	1618	66.42%	-	-	181	119
9889R	Adult	M	No	381	1913	62.97%	-	-	335	231
9890R	Adult	F	No	367	2073	70.87%	-	-	124	85

9891R	Adult	F	No	245	736	37.69%*	-	-	165	128
9892R	Adult	F	No	286	960	42.18%*	-	-	166	122
9893R	Adult	F	No	321	1224	47.81%	-	-	143	123
9895R	Sub-Adult	M	Yes	74	542	92.81%	-	-	1531	1302
9896R	Adult	F	No	231	1711	92.99%	-	-	412	307
9897R	Adult	M	No	323	1221	47.45%	-	-	1311	912
9898R	Adult	F	No	25	126	65.28%	-	-	136	101
9899R	Sub-Adult	M	Yes	67	-	-	101	18.84%	1730	716

* The kill rate estimates used for these cougars (9891R and 9892R) in chapters 4 and 5 were derived from periods where fix success exceeded 45%. Fix success declined precipitously near the end of the collaring period for both of these animals.

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APPENDIX VI

PREDICTIONS OF RATIO-DEPENDENT FUNCTIONAL RESPONSE MODELS DEPEND ON MEASUREMENT UNITS

There has been substantial debate concerning how the functional response (i.e., the rate at which individual predators kill prey) should be incorporated into predator-prey models. In particular, much time and effort has been spent discussing whether prey-dependent or ratio-dependent models are most appropriate (Abrams and Ginzburg 2000). Ratio-dependent models have been criticized because they predict high kill rates by predators at very low prey density provided predator density is also low (Hanski 1991), and because the predator-prey interaction is unstable, making it almost impossible to avoid predicting extinction using ratio-dependent models (Abrams 1994). Yet, ratio dependence has been championed because of its improved fit to data across the range of normal predator and prey densities observed in the field (Vucetich et al. 2002, Jost et al. 2005, Garrott et al. 2007). In this appendix, I evaluate the most popular form of the ratio-dependent model for large carnivores and point out an additional flaw that restricts the utility of the model for predicting predator-prey dynamics. I reiterate Peter Abram's (1994) suggestion that alternative methods for incorporating predator interference into prey-dependent models may permit large carnivore ecologists to move beyond the prey- vs. ratio-dependent debate and develop more robust predictions of functional response. I point to new methods capable of accomplishing this.

METHODS AND RESULTS

I compared the single-species prey- and ratio-dependent forms of Holling's (1959) disc equation. These models are commonly employed to estimate large carnivore functional response (e.g., Vucetich et al. 2002, Jost et al. 2005) and typically take the form:

$$y_t = \frac{aN}{1+aNH} \qquad \text{Prey-dependent}$$

$$y_t = \frac{aN}{P + aNH}$$ Ratio-dependent

where y_t is the kill rate (prey/time), a is the rate of effective search (area/time), N is prey density (no./area), P is predator density (no./area), and H is handling time (time/prey). I fit each model with 2 sets of parameter values for a, P, and N, varying only in the units of measurement (Table VI.1). Handling time was set as a constant across all models at 7 days/prey.

Because search rates, prey densities, and predator densities are identical in each case (except for variation in the units of measurement), one expects no change in model outputs within the prey- and ratio-dependent classes. Indeed, this is exactly what I found for the prey-dependent model (Figure VI.1). For the ratio-dependent model, on the other hand, I discovered that the number of prey expected to die as a consequence of predation varied greatly depending the units of measurement (Figure VI.1). This is a direct result of the variable expression of P in the ratio-dependent model (i.e., >1 or <1), which contrasts with the prey-dependent model where the equivalent term is constant.

Table VI.1: Parameter estimates used to compare prey- and ratio-dependent models. Values were selected arbitrarily and differ only in the units of measurement with which they are expressed.

	Measurement units	
Parameter	**km^2**	**1000 km^2**
a	1	0.001
P	0.02	20
N	0 – 2	0 – 2000

Such large discrepancy in predicted kill rate based on data that are identical for all practical purposes is disconcerting. Especially worrying are the consequences of choice of measurement units for predictions about prey population dynamics when using ratio-dependent models. It is clear that the mechanism behind ratio dependence (i.e., predator interference) is important and probably occurs commonly in nature (Abrams and Ginzburg 2000). However, as I show here, some ratio-dependent model forms are not really a function of the ratio of predator to prey, but rather a function of the value of P. So long as the scale of measurement allows P to be >1, predator interference forces the curve to fall below the prey-dependent curve. If the scale of measurement allows P to fall below 1, then ratio dependence predicts kill rates higher than those expected from a prey-dependent model. Thus, while ratio-dependent models can easily be made to fit data (e.g., Jost et al. 2005) they are much more challenging to apply when attempting to predict the outcome of large carnivore predator-prey interactions because the units of measurement selected by the investigator will change the result. Consequently, traditional ratio-dependent models may not be the best way to integrate predator interference into the functional response. I maintain that allowing the parameters of traditional prey-dependent models to vary as a function of a series of covariates (e.g., Nilsen et al. 2009, Chapter 5), including predator-prey ratios, provides a viable alternative to ratio-dependent models and leaves the pathologies behind.

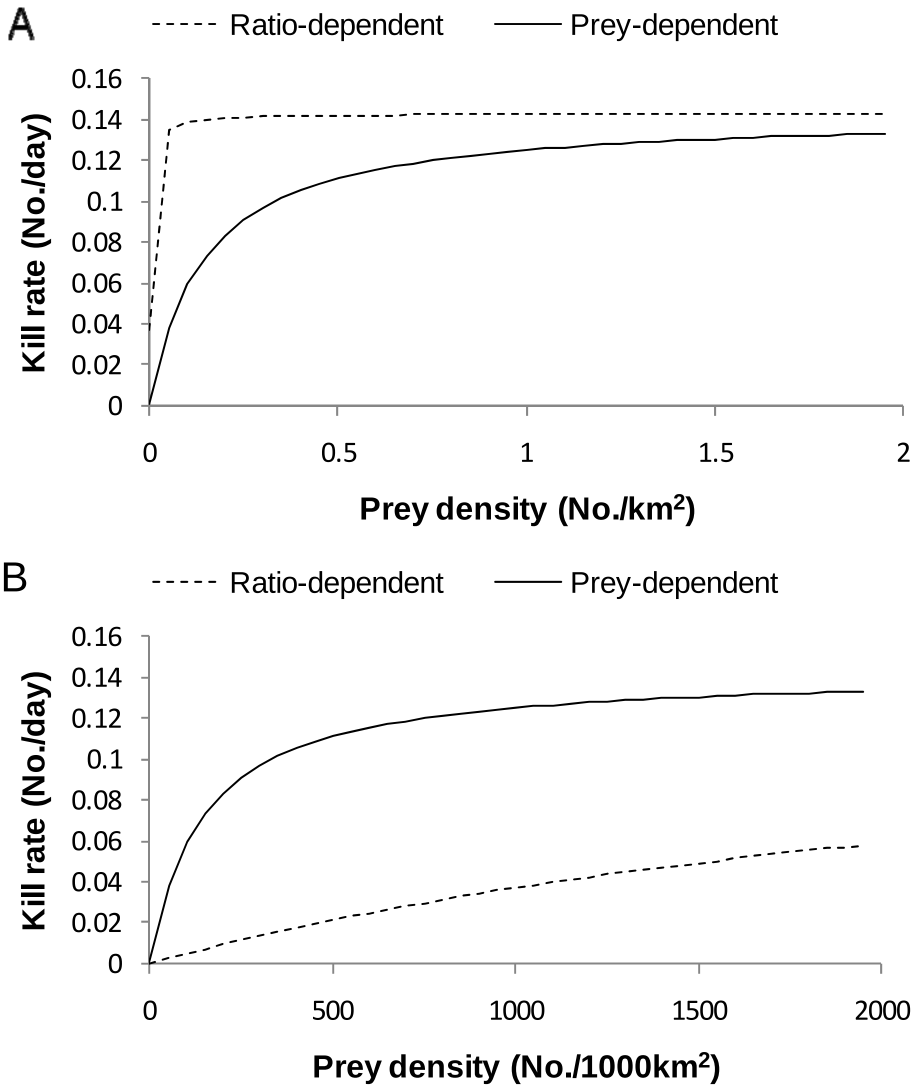

Figure VI.1: Variation in kill rate predictions as a function of prey density for ratio-dependent and prey-dependent functional response models using 2 different units of measurement. All parameter values are identical in each case, but in A parameters are expressed per km^2 whereas in B parameters are expressed per 1000km^2.

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APPENDIX VII

PREFERENCE INFLUENCES PREDATOR-MEDIATED ALLEE EFFECTS IN MULTI-PREY SYSTEMS

Allee effects occur when per capita growth rate of a population declines as a population becomes very small, greatly increasing the probability of extinction (Allee et al. 1949). Predation by generalist predators in multi-prey systems has been advanced as a potential mechanism driving Allee effects (Courchamp et al. 2008). Specifically, because the numerical response of predators to declines in small populations of alternate prey is limited, several authors have suggested that a Type II functional response is sufficient to cause depensatory predation (i.e., the predation rate is inversely density dependent; Messier 1995, Sinclair et al. 1998, Gascoigne and Lipcius 2004). In a recent paper, however, McLellan et al. (2010) used a multi-prey expression of Holling’s (1959) disc equation to point out that predator-mediated Allee effects might be rare in multi-prey systems because efficient predators spend most of their time consuming primary prey and predation on less-abundant secondary prey is largely incidental. McLellan et al. (2010) contend that previous research (e.g., Messier 1995, Sinclair et al. 1998, Gascoigne and Lipcius 2004) failed to account for this effect and therefore might have overestimated the probability of an Allee effect.

Although McLellan et al. (2010) are correct that time spent handling primary prey must be accounted for using an appropriate multi-species functional response (MSFR), they also make the simplifying assumption that the predator does not prefer one prey type over another. Asymmetrical preference (i.e., for some prey types over others) is common in nature due to differences in relative vulnerability among prey types, however, and strong preference may have important implications for the MSFR and for the dynamics of different prey types in multi-prey systems (Sinclair et al. 1998, Cooley et al. 2008, Owen-Smith and Mills 2008). The effects of preference, therefore, should be considered when evaluating the potential for predator-mediated Allee effects to manifest themselves in small populations of alternate prey. In this appendix, I expand McLellan et al.’s (2010) model to incorporate preference and investigate the influence this has on the potential for predators to cause an Allee effect in less abundant prey.

METHODS

McLellan et al. (2010) used the following 2-species form of Holling's (1959) disc equation

$$y_t = \frac{a(N_1 + N_2)T}{1 + a(N_1 + N_2)T_h} \quad \text{Equation VII.1}$$

where y_t is the combined number of both prey types killed per predator per unit time, a is the rate of effective search (km^2/day), N_1 and N_2 are the densities of each prey type, T_h is the time to handle 1 prey, and T is the number of days over which predation occurs. In Equation VII.1, kill rate for each prey species (y_i) can be obtained by multiplying y_t by the proportion of that prey in the environment. I then modified this equation to incorporate preference (Chapter 5).

$$y_t = \frac{a(P_1N_1 + P_2N_2)T}{1 + a(P_1N_1 + P_2N_2)T_h} \quad \text{Equation VII.2}$$

where y_t, N_1 and N_2, T_h, and T are the same as above and P_1 and P_2 are preference values summing to 1 (Joly and Patterson 2003, Chapter 5). To obtain kill rates for each prey type (y_i) in Equation VII.2, one multiplies y_t by $(P_i N_i)/(P_1 N_1 + P_2 N_2)$. In this hypothetical system prey are of the same size and require the same handling time.

McLellan et al. (2010) had in mind a large carnivore-ungulate system where the primary prey (N_1) were deer (*Odocoileus spp.*) and the secondary prey mountain caribou (*Rangier tarandus caribou*). They assigned parameters accordingly: 5 days/prey for handling time, 1km^2/day for search rate, and $T = 30$ days. I used the same parameter values except I made the predator more efficient by assigning a search rate of 10 km^2/day because large carnivores that might prey on mountain caribou (e.g., cougars, *Puma concolor*, and wolves, *Canis lupus*) tend to be highly efficient predators (Dale et al. 1994, Hayes and Harestad 2000, Nilsen et al. 2009, Chapter 5). Following McLellan et al.

(2010), the primary prey (N_1) was set at a density of 1/ km^2 and the alternate prey (N_2) was allowed to vary between 0 and 0.3/ km^2. I also allowed P_1 and P_2 to vary between 0.1 and 0.9 at 0.1 increments for each prey type. To determine total number of prey of each type killed at each combination of N and P, I multiplied y_i by the density of predators in the system, which I obtained using a Type I numerical response of 0.025predators/prey/ km^2. I then divided the number of the i^{th} prey killed by the number of prey of type i available to obtain a predation rate (percent of prey killed in 30 days) and plotted the predation rate against the density for N_2 to determine whether Allee effects were apparent at different preference levels.

RESULTS

Because the predator was efficient, even when $P_2 = 0.9$ and $P_1 = 0.1$, y_t remained close to satiation as N_2 declined from 0.3/ km^2 to 0/ km^2, and proportion of the diet consisting of N_1 increased rapidly (Figure VII.1). Thus, low preference for primary prey did not affect the ability for predators to successfully exploit it. Predation rate for N_2 varied substantially with preference, and strong Allee effects were apparent when the declining alternate prey (N_2) also was the preferred prey (Figure VII.2). Consequently, preference for less-abundant prey allows predation to be strongly depensatory and can drive predator-mediated Allee effects in multi-prey systems. As predator efficiency decreases, depensatory predation becomes less pronounced, and generalist predators may be most likely to cause Allee effects if they also are efficient, as in the case of large carnivores preying on ungulates (Dale et al. 1994, Hayes and Harestad 2000, Nilsen et al. 2009, Chapter 5)

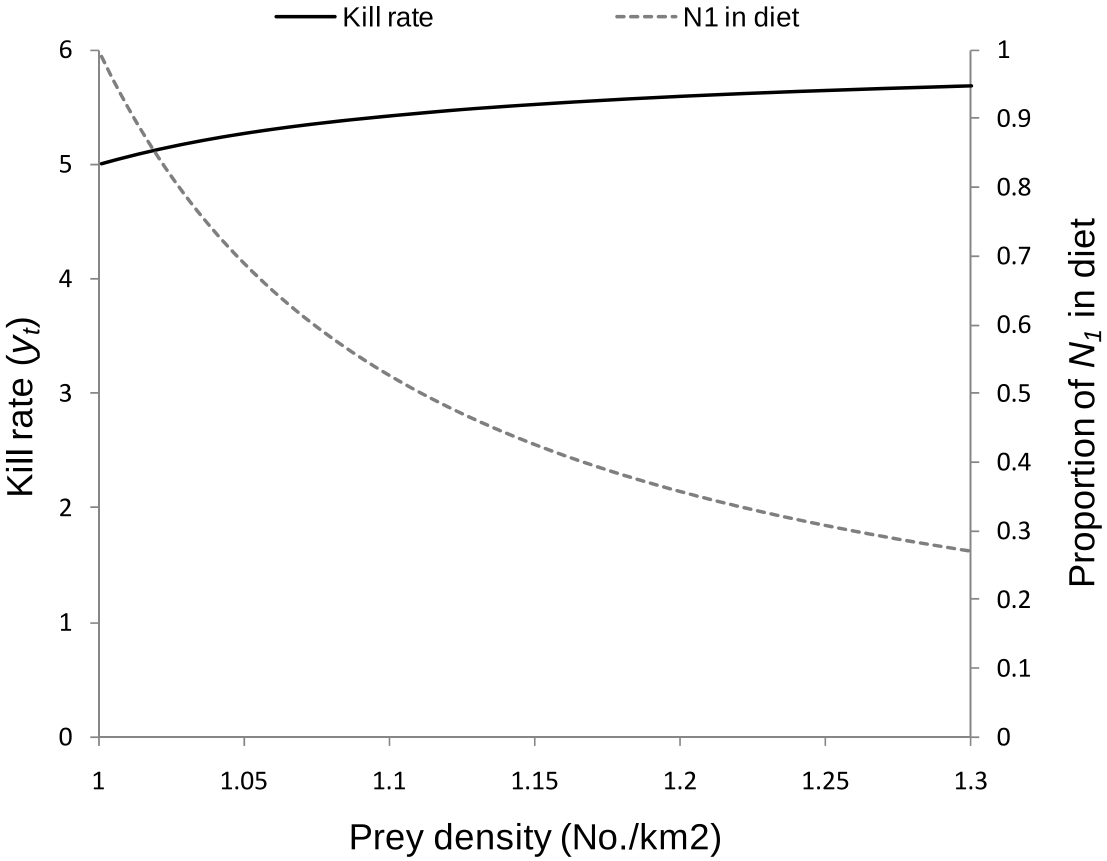

Figure VII.1: Relationship between total prey density and total kill rate (y_t) predicted using equation VII.2 for a declining secondary prey (N_2; 0.3-0/km^2) in a 2-prey system where the primary prey (N_1) maintains a constant abundance (1/km^2), and predators strongly prefer N_2 (0.9) and have a Type I numeric response (0.025predators/prey/km^2). Also displayed is the proportion of N_1 in the diet as a function of declining N_2.

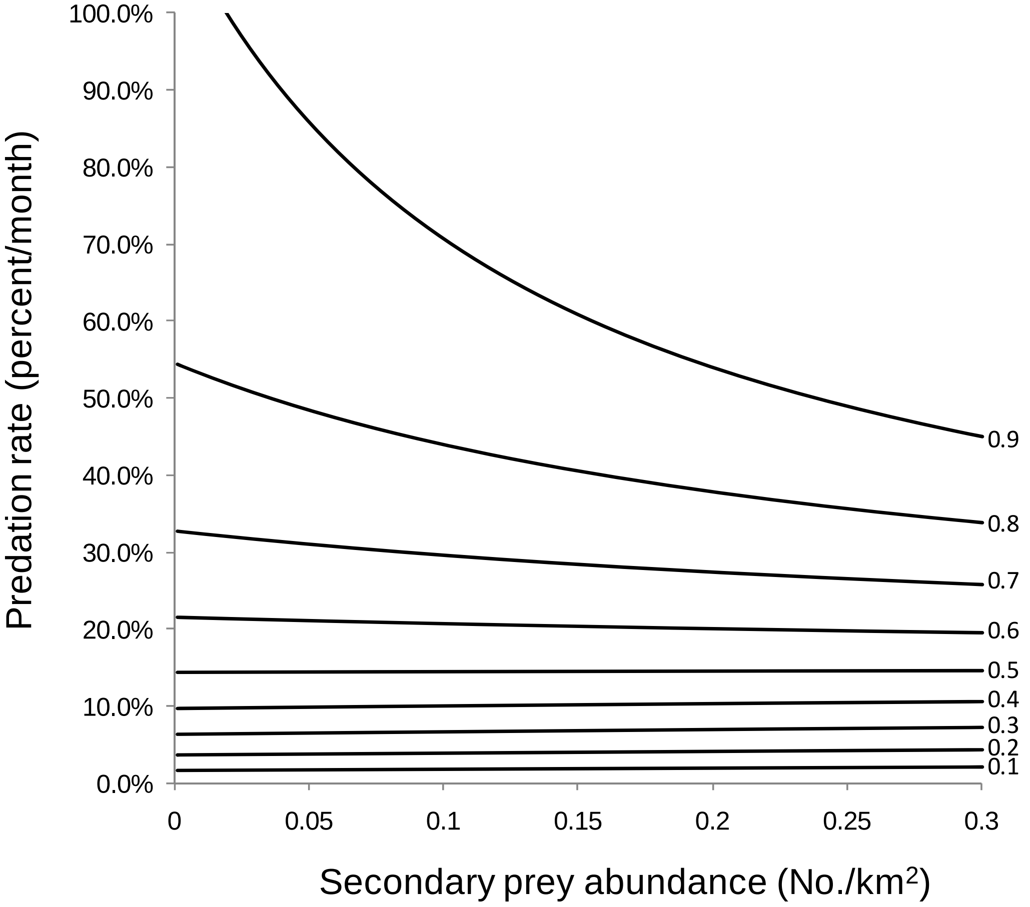

Figure VII.2: Predation rate curves predicted using equation VII.2 at different preference levels (0.1–0.9) for a declining secondary prey (0.3-0/km^2) in a 2-prey system where the primary prey maintains a constant abundance (1/km^2) and predators have a Type I numeric response (0.025predators/prey/km^2).

DISCUSSION

McLellan et al. (2010) correctly point out that predator-mediated Allee effects should be rare in predator-prey systems where more than one prey is present and predators demonstrate equal preference for different prey. This contradicts previous suggestions that predator-mediated Allee effects may exacerbate extinction risk for small populations of prey in multi-prey systems (Sinclair et al. 1998, Gascoigne and Lipcius 2004). However, in this appendix, I show that predator preference is sufficient to produce an Allee effect in multi-prey systems. Thus, where small populations of alternate prey are preferred by a predator, Allee effects may indeed exacerbate extinction risk and so must be considered when evaluating conservation prospects for endangered prey.

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