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Spatial ecology of cougars (*Puma concolor*) in the Cypress Hills: Implications for human-cougar interactions and range expansion

by

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ABSTRACT

Cougar (*Puma concolor*) range is expanding eastward in North America. Understanding how range expansion is occurring in a human-dominated landscape is needed to manage the social and ecological implications of a returning large carnivore. To address this, I used GPS-radio collars and remote cameras to study the habitat and movement ecology of an isolated and recently re-established population of cougars in the Cypress Hills in southwest Saskatchewan and southeast Alberta, Canada. I found that cougars avoided high human-use areas during seasonal peaks in human activity but used these areas according to their availability when human activity was lower. During transience, sub-adult cougars adopted fast-paced nocturnal movements to traverse large stretches of unsuitable (matrix) habitat. The cougar's adaptability to changes in human activity, together with their dispersal capability, will facilitate greater eastward range expansion. This could potentially restore important components of ecosystem structure and function to areas currently devoid of large carnivores.

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CHAPTER 1

GENERAL INTRODUCTION

Large carnivores such as wolves (*Canis lupus*), grizzly bears (*Ursus arctos horribilis*), and cougars (*Puma concolor*) were extirpated from vast portions of their North American range by the early 20th century due to agricultural land use, over hunting of many prey species, and uninhibited direct persecution (Laundré 2012). Socio-political shifts that favour conservation-based wildlife management have occurred within the past several decades. For grizzly bears and wolves these changes in attitudes and management have resulted in recovery programs to maintain and expand their distribution in isolated portions of their range (Shwartz et al. 2002, U.S. Fish and Wildlife Service 2012). In contrast, cougars have begun to naturally re-colonize parts of their former range without any direct human intervention (Larue et al. 2012). In the past two decades, cougar occurrence has increased significantly throughout Midwestern North America and isolated breeding populations have been confirmed in the states of North Dakota, South Dakota, and Nebraska and the province of Saskatchewan (Cougar Network 2007). Expanding carnivore distributions together with increasing urbanization and rural development have resulted in an urgent need for management of human-wildlife interactions. This includes conserving the ecological function of apex predators while considering human-safety concerns and a wide spectrum of public perceptions associated with large carnivores (Riley and Decker 2000).

The return of large carnivores is ecologically beneficial given the regulating effects these species can have on the communities and ecosystems in which they exist (Ripple et al. 2001, Ripple and Beschta 2006). Predators affect prey populations directly through predation or indirectly by restoring a landscape of fear (Brown et al. 1999, Laundré et al. 2010). For example, the reintroduction of wolves to the Yellowstone ecosystem caused a shift in the space-use of elk (*Cervus elaphus*) with cascading benefits to stand recruitment of trembling aspen (*Populus tremuloides*; Ripple et al. 2001, Fortin et al. 2005) and willow (*Salix* spp.; Beyer et al. 2007). Simultaneously, conservation strategies must consider how human development affects these ecological processes. Anthropogenic disturbances can affect wildlife communities through habitat fragmentation, displacement and increased mortality. Human activity on trails has been shown to differentially displace predators and prey (Rogala et al. 2011) potentially altering trophic-level dynamics. Indeed, at larger regional scales, humans have displaced cougars and wolves resulting in cascading effects to woody vegetation through unsuppressed browsing by ungulates (Hebblewhite et al. 2005; Ripple and Beschta 2006, 2008). Therefore, the ecological benefits of expanding carnivore distributions may not be fully realized if human-wildlife interactions are not managed effectively.

Apart from ecological consideration, the return of large carnivores also can be characterized by social and political debate often fuelled by both real and perceived risks to public safety and livelihoods. Although cougar encounters are rare, there has been a marked increase in human-cougar encounters over the last several decades and this trend is expected to continue (Torres et al. 1996, Sweanor and Logan 2010). When these encounters are negative, they often are heavily publicized and sensationalized, which can result in disproportionate perceptions of risk. For example, 55% of respondents to a survey in Clearwater County, Alberta, believed they stood a greater (31%) or equal (24%) chance of being attacked by a cougar than being injured in a car accident (Knopff 2011). Despite some apparent misconceptions, the risk of cohabiting with large carnivores is not necessarily benign. Attacks on people do happen, and more often, so does depredation. In southwest Alberta, for example, cattle comprised 74% of the estimated biomass consumed by wolves during the grazing season (Morehouse and Boyce 2011). Perceptions of risk have been repeatedly shown to influence human acceptance of large carnivores but so can the economic, iconic or spiritual values associated with these species (Riley and Decker 2000, Knopff 2011). For example, 40% of respondents to a survey in Montana believed the presence of cougars enhanced the quality of their life and 69% believed cougars were a sign of a healthy environment (Riley and Decker 2000).

Managing human-carnivore interactions is therefore a multifaceted dilemma merging aspects of ecology and sociology. The early stages of range expansion may pose particular management challenges because little is known regarding the species' ecology in these areas and the risks and values associated with coexisting with predators are not well understood. A better understanding of how range expansion is progressing will provide managers with information required to proactively address these issues and form adaptive management strategies. Cougar dispersal is considered the primary driver facilitating range expansion. Dispersal is required to re-colonize unoccupied habitat patches and maintain the long-term presence and genetic viability of isolated populations (Sweanor et al. 2000, Quigley and Hornocker 2010). Yet remarkably little is known regarding cougar dispersal in the Midwest in part because the phenomenon is relatively recent and also because far-ranging animals have been difficult to track with past radio-telemetry technologies. As a result most cougar dispersal data in grassland-dominated landscapes have focused on coarse measures of movement such as straight-line distance and direction travelled. With advances in satellite communication, researchers can receive GPS-radio collar location data via email which facilitates fine-scale analysis of habitat use and movement of transient animals. This has obvious benefits for increasing our understanding of cougar range expansion and any associated ecological or social implications.

The Cypress Hills are an insular formation of foothills surrounded by the prairies of southeast Alberta and southwest Saskatchewan and represent an excellent case study for examining the implications of cougar range expansion in North America. Historically grizzly bears, wolves and cougars occurred in the Cypress Hills but true to the broad-scale pattern, they were extirpated from the area around the turn of the 20^{th} century. A steady increase in cougar sightings early in the 2000's was the first indication that cougars were re-colonizing this island-like habitat. In 2006, conclusive evidence of breeding was obtained when one family group was detected with remote cameras and another was caught in snares (Bacon 2010). This was the catalyst for research to examine the ecology of this isolated population, which at present is considered the eastern-most confirmed breeding population of cougars in Canada.

Initial research in the Cypress Hills largely examined predator-prey dynamics. Kill site examination and scat analysis determined cougars are opportunistic hunters thereby exposing a multitude of species to predation (Bacon et al. 2011). Deer (*Odocoileus virginianus*, *O. hemionus*) and elk comprise the greatest biomass consumed by cougars and this increased predation risk has restored a landscape of fear for ungulates in the Cypress Hills. Coinciding with the return of cougars, cervid distributions shifted away from forested cover and into the surrounding grasslands apparently as a predator avoidance strategy (Bacon 2010). These results indicate that cougars are fulfilling their role as apex predators by restoring some degree of balance to the Cypress Hills ecosystem. Notably, not a single case of livestock depredation was documented during this survey which has helped ease tensions with local ranchers (Bacon et al. 2011). But ranchers are not the only people who must consider the implications of co-existing with cougars in the Hills.

The Cypress Hills also form the basis for Cypress Hills Interprovincial Park (400km^2) which receives approximately 500,000 visitors annually. The return of cougars to this popular recreation area and the insular nature of the Cypress Hills raise additional questions regarding the potential for human-cougar interactions and the capacity for this population to act as a stepping stone for continued expansion. A better understanding of the cougars' ability to naturally re-colonize patches of habitat and coexist with humans will not only inform an adaptive management strategy to address eastward range expansion of cougars in North America, but also have applications for carnivore conservation and landscape management around the world. Using advancements in GPS collar technology, this thesis examines the spatial ecology of humans and cougars in this shared environment as well as describes the ranging behaviour and dispersal of sub-adult cougars in an isolated population.

In chapter 2, I assess cougar space-use relative to seasonal and spatial variation in human activity. Using data collected by a network of remote cameras I quantify and model seasonal patterns of human activity on the road and trail system within Cypress Hills Interprovincial Park. I use these human activity models as explanatory variables to examine seasonal shifts in habitat selection by cougars. Lastly, I assess cougar use of the trails to examine the potential for direct human-cougar encounters.

In chapter 3, I examine space-use and dispersal of sub-adult cougars emanating from the Cypress Hills. The most active dispersers in mammal populations are usually young males (Chepko-Sade and Halpin 1987) which clearly is true for cougars. I examine the distribution of sub-adult temporary home ranges in relation to known adult range to evaluate hypothesized drivers of dispersal. I then model habitat selection of sub-adults during different ranging behaviours using resource selection functions and assess how landscape variables affect sub-adult movements in a grassland-dominated landscape.

In chapter 4, I provide overall conclusions and offer recommendations for management of this isolated cougar population. My findings and recommendations extend beyond the Cypress Hills with applications for cougar range expansion throughout Midwestern North America. For consistency, all chapters have been formatted following guidelines established by the *Journal of Wildlife Management*.

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CHAPTER 2

HABITAT USE OF A RE-COLONIZED COUGAR POPULATION IN RESPONSE TO SEASONAL FLUCTUATIONS OF HUMAN ACIVITY

INTRODUCTION

Cougar (*Puma concolor*) sightings have been on the rise across much of Midwestern North America as cougars re-colonize parts of their former range through eastward expansion (Cougar Network 2007, Rosatte 2011, LaRue et al. 2012). Cougar range expansion and growing urbanization is increasing human-cougar interactions (Torres et al. 1996, Sweanor and Logan 2010, LaRue et al. 2012). More emphasis on managing human-cougar interactions is needed to maintain the cougar's ecological role as an apex carnivore, while considering human-safety concerns and public tolerances associated with large carnivores (Riley and Decker 2000). Managing human-cougar interactions in the early stages of cougar re-colonization poses a unique set of challenges. Little is known locally regarding the species' ecology and in some areas the public has not considered the implications of carnivore coexistence for almost a century. At present, it remains unclear how the cougar's eastward expansion will progress and be tolerated socially.

Understanding the spatial ecology of cougars around people and human-developed habitats is important for mitigating human-cougar interactions for several reasons: it is fundamental for understanding public-safety risks posed by cougars (Arundel et al. 2007); it will assist with managing the impacts of human activity on cougar ecology (Arundel et al. 2007); it provides a basis for public education initiatives (Arundel et al. 2007); and it will be critical for developing pre-emptive and adaptive management strategies in areas currently experiencing cougar re-colonization or areas where it is likely to occur (Cougar Management Guidelines Working Group 2005, Arundel et al. 2007).

Cougars are habitat generalists although a number of habitat characteristics appear to be important to the biology of the species (Kertson et al. 2011). As stalking predators, cougars tend to prefer rugged terrain with some form of lateral cover, such as forest, shrub, or rocky outcroppings (Logan and Irwin 1985, Arundel et al. 2007). A strong propensity for ecotone edges also has been widely documented (Holmes and Laundré 2006, Laundré and Loxterman 2007, Knopff 2011). Cougar response to anthropogenic disturbances is particularly relevant for understanding human-cougar interactions. In general, cougars appear relatively resilient to human disturbance to a degree. Research examining cougar movement and habitat use across a gradient of human development suggests an adaptive response by cougars, indicating human-dominated landscapes represent modified, not necessarily unsuitable, habitat (Kertson et al. 2011, Knopff 2011). Knopff (2011) reported a functional response by cougars where an increase in human disturbances resulted in cougars using modified habitats more frequently. In some cases, cougars have been documented using human infrastructure, such as gravel roads and trails, as likely travel corridors (Dickson et al. 2005, Kertson et al. 2011). However, cougars are not pliant to all intensities or scales of disturbance. High density residential development and highways have proven to be effective barriers to movement and should still be considered unsuitable habitats (Maehr et al. 2002, Dickson et al. 2005, Arundel et al. 2007, Kertson et al. 2011) and increased human activity has been demonstrated to sufficiently displace cougars creating prey refugia resulting in trophic-cascades (Ripple and Beschta 2006, 2008).

The cougars’ relative resiliency to human disturbances is a key factor facilitating their eastward range expansion but likely also contributes to the significant increase in human-cougar interactions observed over the past two decades (Torres et al. 1996, Sweanor and Logan 2010). In addition, behavioural and ecological responses by cougars to human development also are more likely related to human activity rather than physical infrastructure (Arundel et al. 2007). Relying on measures of infrastructure as a proxy for human use may therefore over simplify spatial and temporal complexities of human activity limiting the effectiveness of management strategies designed to mitigate human-wildlife interactions (Northrup et al. 2010). Despite this, few studies have quantified spatio-temporal variations in human activity to examine the effects on cougar spatial ecology (Sweanor et al. 2008). No studies have done so for a re-established cougar population east of their contemporary range.

Parks and protected areas often serve a dual role of providing recreational opportunities for people while preserving the area’s ecological integrity. In northern latitudes, these natural areas often receive dramatic fluctuations in seasonal human use due to the comparatively harsh winter climate that limits visitors. This makes them excellent systems in which to study human-wildlife interactions. Cypress Hills Interprovincial Park straddling the Alberta and Saskatchewan border has recently been re-colonized by cougars and hosts the eastern-most confirmed breeding population in Canada. Cougar sightings increased significantly in the early 2000's coinciding with the cougar's return (Bacon 2010). My research sought to examine how seasonal fluctuations of human activity affect cougar spatial ecology in Cypress Hills Interprovincial Park. Specifically, my objectives were to: 1) quantify seasonal variation in human use and model the within-season spatial distribution of motorized and non-motorized human activity; 2) use models of motorized/non-motorized activity to examine seasonal effects on cougar habitat selection; and 3) assess how spatial-temporal variation in human activity affects cougars' use of roads and trails.

STUDY AREA

Cypress Hills Interprovincial Park (CHIP, 400 km^2, Fig. 2.1) is located in southeastern Alberta and southwestern Saskatchewan, Canada. CHIP encompasses a large portion of the Cypress Hills, an insular formation of foothills which rise several hundred metres above the surrounding grassland landscape. The hills are further distinguished from their surroundings due to their abundance of tree cover consisting primarily of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*). The matrix surrounding the hills is an expanse of mixed grasslands, ranchlands and agriculture development. The Cypress Hills' relatively high elevation (1,234 m, Elkwater, AB) results in cooler summers and warmer winters than the surrounding low lands – the average temperature is 19.1 C in July and -3.3 C in

January. Annual precipitation is 533.5 mm which also is greater than the surrounding area.

CHIP is managed by two provincial government agencies – Saskatchewan Tourism Parks Culture and Sport and Alberta Tourism Parks and Recreation. The Saskatchewan portion is comprised of two separate areas known as Center Block and West Block. The Alberta portion is a single protected area known as CHIP Alberta (Fig. 2.1). In total, approximately 500,000 people visit CHIP annually, although this visitation is highly seasonal. Two core areas of human activity occur in the park. One is located on the Alberta side (Elkwater) and one on the Saskatchewan side in Center Block. Over 1,000 campsites, 500 cottages and multiple business leases operate in CHIP with most occurring in the two core areas. Relevant to this study, there is an extensive network of roads and trails (hereafter trails) that are maintained for visitors. The average distance to the nearest trail in CHIP is 509m (SD = 550m, min = 0m, max = 3,900m; n = 4,000 random locations). Trails can be categorized into 5 types: winter roads (usually paved and actively ploughed during winter), summer roads (usually paved but not ploughed), secondary roads (usually gravel), truck trails, and hiking trails, some of which are track-set for cross-country skiing in winter. Motorized traffic is restricted to roads and truck trails while hiking, biking, cross-country skiing and equestrian use comprise the bulk of non-motorized activity on trails. Apart from winter roads, gates and/or snow conditions limit motorized access in the winter months to most trail types although some become popular for non-motorized activities.

The closest known breeding populations of cougars to CHIP are 200 km south in the Bear Paw Mountains in Montana and 250 km west in the Rocky Mountains of southwestern Alberta. Primary diet of cougars in the Cypress Hills is white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), porcupines (*Erethizon dorsatum*) and elk (*Cervus elaphus*) (Bacon et al. 2011, Morrison unpublished data).

METHODS

Measuring human activity

A network of 90 remote camera stations was maintained between 1 July 2011 and 30 June 2012 to quantify human use on trails in CHIP. To ensure an adequate spatial distribution of sample locations, the park was overlaid with a 500×500m grid and 90 cells were randomly selected for sampling. Within each cell a random point was generated and 'snapped' (i.e., relocated) to the nearest trail defined as secondary roads, truck trails, and hiking trails. Winter roads and summer roads received relatively high amounts of traffic (based on expert opinion from park staff). These trails were excluded from sampling to reduce the potential of camera theft and vandalism. Actual camera stations were established at the nearest suitable tree to the random location. Trees were identified with a metal tag and marked with a handheld Global Positioning System (GPS) so they could be relocated for subsequent sampling periods throughout the year.

The year was divided into 6 two-month sampling periods knowing that July and August were the busiest months in park visitation. The sampling periods were therefore January-February, March-April, May-June, July-August, September-October, and November-December. Thirty cameras (RECONYX, Creekside, WI) were cycled on a 20-day rotation to sample all 90 camera stations during each 2-month period. I made the assumption that data recorded during the 20-day sampling session would be representative of the 2-month period. The order of sampling for camera stations was chosen at random within each period. In the field, cameras were positioned at a height approximately 1 m above the surface of the trail and aimed approximately 60 degrees across the trail. Branches and brush were cleared from the camera's field of view to limit the number of environmental triggers. The cameras were programmed at the highest sensitivity and to take three photos, three seconds apart, for every triggered event. A 15-second quiet period was then enforced between triggers. At the end of the scheduled sampling period, field crews would replace memory cards and batteries and move the camera to the next station to be sampled.

All remote camera data were processed using Timelapse Image Analyzer (Greenberg and Godin, 2012). Photos of human activity were categorized as motorized (vehicles, ATVs and snowmobiles) or non-motorized (foot, bike, ski and equestrian) and the date, time and number of individuals (e.g., 2 hikers = 2; 1 car regardless of passengers = 1) were recorded. Events that lasted for more than one trigger, where the individual(s) was clearly attracted to the camera, were recorded as a single observation. On occasion, sampling sessions did not last the entire scheduled duration due to environmental disturbance, human tampering, or equipment malfunction. In these cases the sampling period ended on the date of the last recorded photo or when the field of view was altered significantly. To account for fine-scale temporal variation in human use during the sampling session (e.g., holiday weekends) only sessions that were operational for a minimum of 13.5 days were included in the analysis. This ensured the greater portion of each day of the week was included in the sampling session at least twice to smooth out any isolated variability in human activity.

Seasonal models of human activity

To assess seasonal variation in human use I calculated an index of overall human relative activity (motorized and non-motorized combined; hereafter overall activity) at each camera station for each two month period. Overall activity was calculated as the sum of individuals observed during each trapping session divided by the number of trap days that the camera was operational (George and Crooks 2006). Because human use data were right skewed, a natural log transformation was performed prior to statistical analysis. A Friedman's Rank Sum test was used to test for differences in overall activity between 2-month periods. Following any significant results, a pair-wise Wilcoxon tests was used with a Bonferonni corrected P-value = 0.003 to determine which specific periods differed. Periods that did not differ significantly and had similar environmental conditions were pooled into a single season. The resulting seasonal definitions formed the basis of subsequent models of human activity and cougar habitat selection.

To estimate within-season spatial variation of human activity, indices for motorized (MRA) and non-motorized (NMRA) relative activity were estimated separately using the same method described above for overall activity. Generalized linear models (Gaussian distribution) were then developed for MRA and NMRA within each season using a set of candidate models. Candidate explanatory variables were determined in consultation with park officials. Descriptions of covariates are listed in Table 2.1. If explanatory variables were highly correlated ($|r|>0.7$) they were restricted from entering the same model. In each season the most-supported model for MRA and NMRA was chosen based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002).

Using the most-supported models, I estimated seasonal MRA and NMRA for each season throughout the trail network of the park to develop spatial layers for subsequent cougar habitat selection models. To do so, I distributed locations along the trail network layer at a maximum distance of 30 m. At each point I estimated MRA and NMRA using the respective most-supported model for the season in question. For winter roads and summer roads that were not included in the camera survey, I assigned the highest estimated value for MRA rounded to the first decimal place. This provided a value slightly larger than all other point estimates which was satisfactory for a relative activity index, although it is likely still an underestimate of actual motorized use for these trails. For NMRA, winter and summer roads were combined with a reference category (secondary roads). The resulting spatial layers were then used as candidate explanatory variables for modeling seasonal cougar habitat use.

Cougar capture and collaring

Between 2008 and 2011, cougars were captured in the CHIP area. Cougars were pursued and treed with the assistance of a professional houndsmen and trained tracking hounds, chemically immobilized, and fitted with a GPS-radio collar (Lotek Model 4400; ATS Iridium). All animal handling was done by trained personnel in accordance with Animal Use Protocol 568-02-11 approved by the University of Alberta Animal Care Committee. GPS collars were programmed to take a fix every 3 hrs. Only GPS relocations that occurred within the CHIP boundary were included in this analysis because this was the extent of the human activity models. Only independent cougars that registered a minimum of 50 GPS relocations in a season were included in the analysis for that particular season (Manly et al. 2002).

Cougar habitat modeling

I used a two-stage modeling approach to examine individual and population level response of cougars to seasonal variation of human activity (Nielsen et al. 2002, 2009; Fieberg et al. 2010). For each season resource selection functions (RSF) were estimated for individual cougars, using logistic regression, to quantify relative probability of a site being selected based on multiple explanatory variables (Table 2.2; Manly et al. 2002). Use data were determined by cougar GPS locations that fell within the CHIP boundary and were separated into seasons based on local date and time (Central Time Zone; GMT-6). Within each season, the domain of availability was delineated by buffering each

GPS location by 2,062 m, which was the 95th percentile of 3-hr step lengths observed within the CHIP boundary (Morrison unpublished data). These buffers were dissolved to create one polygon representing the seasonal home range and then clipped by the CHIP boundary to ensure no available locations were drawn from outside of the study area. The extent of the resulting polygon was used to draw a sample of available points at a 5:1 ratio to observed points for each cougar's seasonal distribution. This use-availability design provides a measure of patch selection at the seasonal home range scale (level III, Johnson 1980).

Five *a priori* candidate models examining environmental and anthropogenic variables were hypothesized to affect seasonal cougar habitat selection (Table 2.3). See Table 2.2 for a description of covariates. Model *Enviro* included only environmental covariates to test if the inclusion of anthropogenic covariates in subsequent models improved model performance. Environmental covariates were chosen based on characteristics deemed important to the biology of species from past research studies (Logan and Irwin 1985, Arundel et al. 2007, Kertson et al. 2011). Model *Trail* expanded on *Enviro* to include distance to the nearest trail, representing the most basic measure of human activity. Models *Motor_RA*, *Non-motor_RA* and *Combined_RA* expanded on *Trail* to include seasonal estimates of MRA and NMRA obtained from my models of human use (Table 2.3).

Candidate models were first estimated for each individual cougar and ranked according to AIC scores (Burnham and Anderson 2002). AIC weights (w_i) were then averaged across individuals to determine the best ranked population-level models in each season. In all seasons, one model consistently ranked as most supported based on AICw_i. Therefore, beta coefficients were averaged across individual models for this single model structure to estimate population-level coefficients. Based on the sample of individual betas, I then calculated 95% and 85% confidence intervals for coefficients to examine population-level trends in selection and levels of significance.

Cougar use of trails

To investigate the relative use of trails by cougars in each two-month sampling period, camera data were summarized for cougar activity following the same protocols used to quantify seasonal human activity. I examined how many camera stations detected a cougar, the average relative activity of cougars and the distribution of detections with respect to time of day (morning, day, evening and night). To ensure equal detectability between periods, only camera stations that were operational in all 6 two-month periods were included in this analysis (n=61). Diurnal periods were defined 1 hour after sunrise and 1 hour before sunset using seasonal sunrise/sunset times for Medicine Hat, AB, (www.nrc-cnrc.gc.ca) at the mid-point of each trapping session. The nocturnal period was defined by the start and end times of civil twilight, with the crepuscular periods of morning and evening falling between night and day. In each season, I multiplied the total number of detections by the proportional duration of each day-period to obtain the expected distribution of detections assuming indiscriminate day-period use of the trails. I calculated ratios of observed to expected frequencies in each day-period in each season to examine cougar selection for diel periods. I averaged these selection ratios across all seasons to examine general trends in cougar use of trails.

To examine the trail-level effects of seasonal human activity on cougar use of trails, I compared average MRA and NMRA at sites that detected a cougar versus stations that did not detect a cougar using t-tests. I ran a second round of t-tests only on sites that detected a cougar to determine if average MRA and NMRA differed between locations that observed a cougar during the day compared to sites that observed a cougar at night. If a site recorded both day and night detections it was assigned to the day-time group.

RESULTS

Measuring and modeling human activity

Camera stations were operated for an average of 19.26 days during each 2-month period and recorded 28,997 total human activity events. See Table 2.4 for summary statistics by season. Five camera stations were excluded from analysis because they were compromised in some fashion (e.g., due to changes in route access during the yearlong sampling period).

Overall human activity measured during 2-month sampling periods in CHIP fluctuated significantly throughout the year (χ^2 = 141.98, df = 5, P< 0.005). A dramatic annual cycle in human use was present peaking in July and August and accounting for 58% of the total year-round human use (Table 2.4). May-June and Sep-Oct periods received moderate levels of human use representing 14% and 15% of the annual total respectively (Table 2.4). Jan-Feb and Mar-Apr periods received the lowest annual human use at 2% each (Table 2.4). Nov-Dec period represented a transition between fall and winter with 8% of annual activity (Table 2.4). Relative activity therefore followed an annual cycle with the most activity in July-Aug (Fig. 2.2). There was no significant difference in overall activity between Sep-Oct and May-June (Fig. 2.2). These two periods were not pooled, however, to control for considerable environmental variation between these times of year. No significant difference in overall activity was found between Jan-Feb and Mar-Apr (Fig. 2.2). Both of these periods were subsequently pooled into a single season because they were more similar in environmental conditions. Relative activity in Nov-Dec differed significantly from all other periods (Fig. 2.5). Given these results, all subsequent human use and cougar RSF models considered 5 separate seasons: winter (Jan-Feb, Mar-Apr), spring (May-June), summer (July-Aug), fall (Sep-Oct), late-fall (Nov-Dec).

The most-supported seasonal models for MRA and NMRA are provided in Table 2.5. Trail type was the only covariate to consistently appear in both MRA and NMRA models across all seasons. Based on these seasonal models, spatial layers of MRA and NMRA were estimated across the trail network to serve as a covariate in seasonal cougar RSF models.

Seasonal cougar habitat selection

Fifteen cougars (5 males; 10 females) with >50 GPS locations in CHIP for at least one season were used to assess seasonal habitat selection and response to human activity (see Table 2.6 for summary of cougar sample sizes and average number of GPS relocations by season). At the individual level, all models in all seasons that included anthropogenic measures outperformed null habitat models that included only environmental covariates (Table 2.3). Also, models that included estimates of human activity (*Motor_RA, Non-motor_RA, Combined_RA*) at the nearest trail consistently outperformed models which only incorporated distance to nearest trail (Table 2.3). *Combined_RA*, which included estimated MRA and NMRA, was the most supported in all seasons and thus used to estimate population-level models (Table 2.3).

At the population level, cougars demonstrated positive selection for rough terrain in all seasons although not significantly-so in spring. Although forest cover was not strongly selected by cougars in any season except winter, there was strong positive selection for proximity to forest edge, especially when cougars were in open habitats (Table 2.7A). Selection for hydrological features was variable in terms of direction and significance between seasons.

In response to anthropogenic features, individual responses by cougars were highly variable, although seasonal trends were apparent. Cougars were positively associated with proximity to trails in winter and negatively associated with proximity to trails in summer. During the shoulder seasons of spring, fall and late-fall, no strong effect for proximity to trails was supported (Table 2.7A). Of the 6 individual cougars included in both summer and winter models, 3 cougars demonstrated a shift in selection congruent with the population-level shift. One cougar shifted opposite to the population-level response, one cougar maintained its negative selection between seasons and one cougar maintained its positive selection between seasons. Across most seasons there was a general trend of avoidance of areas in proximity to greater levels of MRA and NMRA, although this response was only significant in spring for MRA and NMRA and in summer for NMRA (Table 2.7A). A great deal of variation at the individual level was observed in response to human activity covariates. Selection varied between cougars within each season and varied within individual cougars between seasons (Table 2.7B).

Cougar use of trails

Remote camera surveys recorded 267 cougar detections at 51 (82%) of the camera stations. Cougars were detected at the greatest number of camera stations in Sep-Oct followed in descending order of detections by Nov-Dec, July-Aug, Jan-Feb, May-June and Mar-Apr (Fig. 2.3). Relative activity of cougars was likewise highest in the fall, summer and late-fall months and lowest in spring and winter (Fig. 2.4). Although these data indicate a general seasonal trend with greater use in summer and fall months compared to winter and spring months, pair-wise Wilcoxon tests of cougar RA were significantly different in cougar relative activity only when comparing Sep-Oct between Jan-Feb, Mar-Apr and May-Jun (Fig. 2.4). While Bonferonni corrections preserve the experiment-wise power of detecting type I errors, the power of detecting type II errors is reduced.

Averaged across all seasons cougars were detected 2.03 times more than expected in the evening and 1.42 times more than expected during the night. They were detected less than expected in the morning and day by .94 and 0.55 times respectively (Table 2.8). Cougars were detected less on trails during the day in May-Jun, Jul-Aug and Sep-Oct compared to the seasonal average. Cougars were considerably more active on trails at night during summer which was the peak period in human activity (Table 2.8). Average MRA was marginally higher at camera stations that detected a cougar in summer ($P = 0.049$). Otherwise, within-season MRA and NMRA was not significantly different between locations that detected a cougar and those that did not (in all cases, $P > 0.05$). Similarly, for locations with cougar detections, MRA and NMRA did not significantly differ between day and night-time periods (in all cases, $P > 0.05$).

DISCUSSION

Human activity

Human activity in the Cypress Hills peaked in the summer months of July and August receiving over half (58%) of the total year-round activity and 27 times the activity observed in winter months (January - April). This exemplifies the oscillating pattern of human activity in natural areas in northern climates. By stratifying subsequent cougar habitat analyses into 5 seasons based on this oscillation I accounted for the effects of seasonal variation in human activity on cougar space-use that may otherwise be overlooked at different temporal scales.

Within-season spatial variation of motorized and non-motorized relative activity was explained most consistently by trail type although other covariates that improved the model included distance to core areas, entry gates or trailheads. This suggests that infrastructure as a surrogate for spatial variation in human use can be used when empirical data is not available although caution should be used when interpreting results (Northrup et al. 2010).

Seasonal cougar habitat selection

My primary objective was to examine cougar space-use relative to temporal (between seasons) and spatial (within season) variation in human activity. In this regard the same suite of environmental covariates was included in all candidate models to test the hypothesis that anthropogenic covariates would improve model performance. Managers and the public should not overlook however, the importance of recognizing natural habitat characteristics as a means of reducing the potential for negative human cougar interactions. Increasing human presence in prime cougar habitat degrades habitat suitability for cougars and increases the probability of an encounter (Arundel et al. 2007). Results for natural habitat covariates are largely congruent with findings elsewhere. In all seasons, cougars in Cypress Hills Interprovincial Park generally preferred rugged forested terrain and had a slight affinity to edge habitats. This selection for edge was strongest when in open habitats indicating cougars did not venture far from forest cover. Managers can use this information to limit human cougar interactions by focusing human activities (e.g., trails, campsites, day-use areas) in less preferred habitats.

Cougar response to seasonal variation in human activity.- At population levels, cougars shifted their habitat selection based on seasonal fluctuations of human activity. Cougars selected for areas farther from trails during the summer when overall relative activity averaged 8.72 humans per day. Moderate relative human activity, ranging from 2.53 to 1.37, appeared to have little impact on cougar habitat selection. When the average relative human activity was below 0.36, cougars selected for areas closer to trails. By providing a quantifiable basis of human activity my results expand on other studies that have demonstrated flexibility in cougar spatial ecology in response to anthropogenic disturbances (Kerston et al. 2011, Knopff 2011, Janis and Clark 2002). My results highlight the importance of quantifying human activity and support the hypothesis that it is human activity, rather than physical infrastructure, which affects cougar spatial ecology (Arundel et al. 2007).

One of the few studies to quantify human activity observed variable responses by cougars to weekly fluctuations in human activity in a California park (Sweanor et al. 2008). Some cougars appeared to avoid areas of high human use while others used the park randomly (Sweanor et al. 2008). Quantifying human activity at a larger temporal scale (i.e., seasonally versus weekly) might give cougars more time to adjust their selection of habitats. For example, cougars in Florida avoided roads during the hunting season coinciding with an expected increase in human activity during this period (Janis and Clark 2002). Conversely, studies have documented cougars being more tolerant of human development at night when human activity is presumably lower indicating cougars are able to adapt to fine-scale temporal patterns in human use (Ruth 1991, Orlando et al. 2008, Knopff 2011).

The seasonal shift in selection I observed has important implications for understanding human-cougar interactions since the potential for spatial-temporal overlap of people and cougars could be maximized at moderate or low levels of human activity (Sweanor et al. 2008, Kertson et al. 2011). For example, several instances of cougars killing and caching deer under cottages and decks have been observed during the winter season when human visitation is low and many cottages are vacant. This behavior likely contributes to the positive selection for proximity to roads that was observed in the most-supported winter habitat model. The cougars' willingness to enter high human development areas to acquire food further supports the hypothesis that cougars avoid human activity rather than infrastructure and in some cases infrastructure may be selected for certain behaviours such as feeding. In one instance, a cougar killed a deer in the forest and dragged it for 375 m into the cottage subdivision to cache it under a deck.

This highlights an important consideration in understanding human-cougar interactions which is the effect of human activity on prey. A spatial shift in prey distribution due to human activity could reasonably explain some of the seasonal variation I observed in cougar habitat selection. Ungulates have been documented to shift away from high human use trails in the Rockies (Rogala et al. 2011). If prey species in CHIP respond similarly this might contribute to the shift observed in cougar habitat use. Conversely, other human behaviors, such as providing feed for deer through the winter, can result in a concentrated abundance of prey and may attract cougars, which is supported by my field observations of cougars using the core area in winter. Failure to consider this predator-prey relationship may overestimate the direct effect of human activity on cougars. In my study area there is no empirical data on the seasonal distribution of prey and so my ability to account for this variable was limited. Including environmental covariates important to the biology of cougars, which necessarily includes predation, should assist in isolating the variation in cougar space-use associated with anthropogenic covariates.

Cougar response to within season spatial variation of estimated human activity.- At the population level, cougars were less sensitive to the spatial distribution of motorized and non-motorized human activity within each season. Although a weak trend of avoidance was observed towards greater levels of MRA and NMRA in all seasons, this avoidance was only significant for MRA in spring and for NMRA in spring and summer. The over-all lack of significance at the population-level reflects the wide variation of selection observed at the individual level. Individual variation in selection has been documented for cougars in other habitat selection studies in response to anthropogenic development (Sweanor et al. 2008, Kertson et al. 2011, Knopff 2011).

A potential source of this individual variation is that GPS data were collected during all possible cougar behaviours. Certain behaviours, such as feeding or bedding, can localize a cougar for an extended time period creating a cluster of GPS points (Knopff et al. 2009). Because my sampling design assigned the estimated MRA and NMRA of the nearest trail to each GPS point, a cluster of GPS points could influence apparent selection. Other studies have focused on behaviour specific modelling and have observed differences in selection accordingly (Knopff 2011). Because I was interested in overall habitat selection I was justified in including all behaviour types in my cougar habitat modelling. Two-stage modelling corrects for this potential bias by treating the individual as the sample unit (Nielsen et al. 2002, 2009; Fieberg et al. 2010). My population-level results then accurately reflect an over-all indifference to the spatial distribution of human activity with a weak general trend of avoidance in most seasons and a stronger response in summer and spring when human activity was higher.

Cougar use of trails

RSFs are an effective method for understanding how human activity affects wildlife spatial ecology (Hebblewhite and Merrill 2008). Examining cougar use of the trails, on the other hand, provides insights into the potential for direct interactions with people. Although I was limited to one year of data on cougar use of the trails, and therefore the generality of my results is limited, these findings provide baseline information for the public and wildlife managers to consider when examining the potential for human-cougar interactions.

Cougars were detected at 81% of randomly distributed camera stations indicating cougar use of trails is prevalent in CHIP. Interestingly, cougars were detected at more camera sites and were slightly more active on trails during the summer and fall periods even though they tended to avoid areas near trails in these peak tourist months. Although cougars may avoid these features at a larger spatial scale, trails may still be important travel corridors to facilitate movement through dense vegetation (Beier 1995, Dickson et al. 2005, Kertson et al. 2011). Stratifying the habitat models into day and night might reveal differential selection. Indeed, cougars were detected relatively more on trails at night during Jul-Aug, and less during the day in May-Jun, Jul-Aug and Sep-Oct which could be indicative of a fine-scale temporal shift to more nocturnal use of the trails when human activity peaks. Diel shifts in cougar spatial ecology and activity, based on presumed shifts in human activity, have been documented in other studies (Van Dyke et al. 1986, Ruth 1991, Orlando et al. 2008, Knopff 2011).

With the exception of MRA in the summer, there was no significant difference between MRA and NMRA observed at camera stations that detected a cougar versus those that did not, or detected a cougar during the day versus at night. These results support my findings that indicate within-season spatial variation of human activity had little effect on cougar habitat selection. Instead, cougars were detected at more camera sites in the evening and the night, regardless of season or observed human activity, which is likely a reflection of the crepuscular and nocturnal ecology of the species (Van Dyke et al. 1986, Sweanor et al. 2008). Autocorrelation functions of step length for cougars showed a weak 24 hr periodicity providing additional support that cougar movement has daily patterns (Boyce et al. 2010). The cougars naturally divergent schedule with human activity, which peaks during the day, is likely a key factor why cougars are able to coexist in close proximity to human development with relatively little conflict or interactions. Sweanor et al. (2008) points out that crepuscular periods, when cougar activity is waxing and human activity is waning, might have increased encounter potential. This supports the hypothesis that human-cougar interaction could be greatest at moderate levels of activity. Importantly these results highlight that the potential for human-cougar encounters is present throughout the year.

Management and conservation implications

This study of a recently re-established cougar population in Cypress Hills provides a quantitative assessment of the flexibility of cougar spatial ecology at a seasonal scale. The dramatic fluctuation in human activity observed and the resulting shift in cougar space-use underscore the importance of carefully considering temporal scale when investigating human-wildlife interactions.

Managers and the public should be aware that cougars are able to adapt to variable amounts of human activity. Although this has meant conservation gains for the species in terms of eastward range expansion, it also means a potential increase in human-cougar interactions and novel challenges for wildlife managers. Managers and the public should recognize that the potential for human-cougar interactions is always present, however there may be periods, such as low human-use seasons and evenings, when the potential is greatest. Although I documented seasonal trends in selection at the population level, the amount of variation observed at the individual level makes these human-cougar interactions difficult to predict.

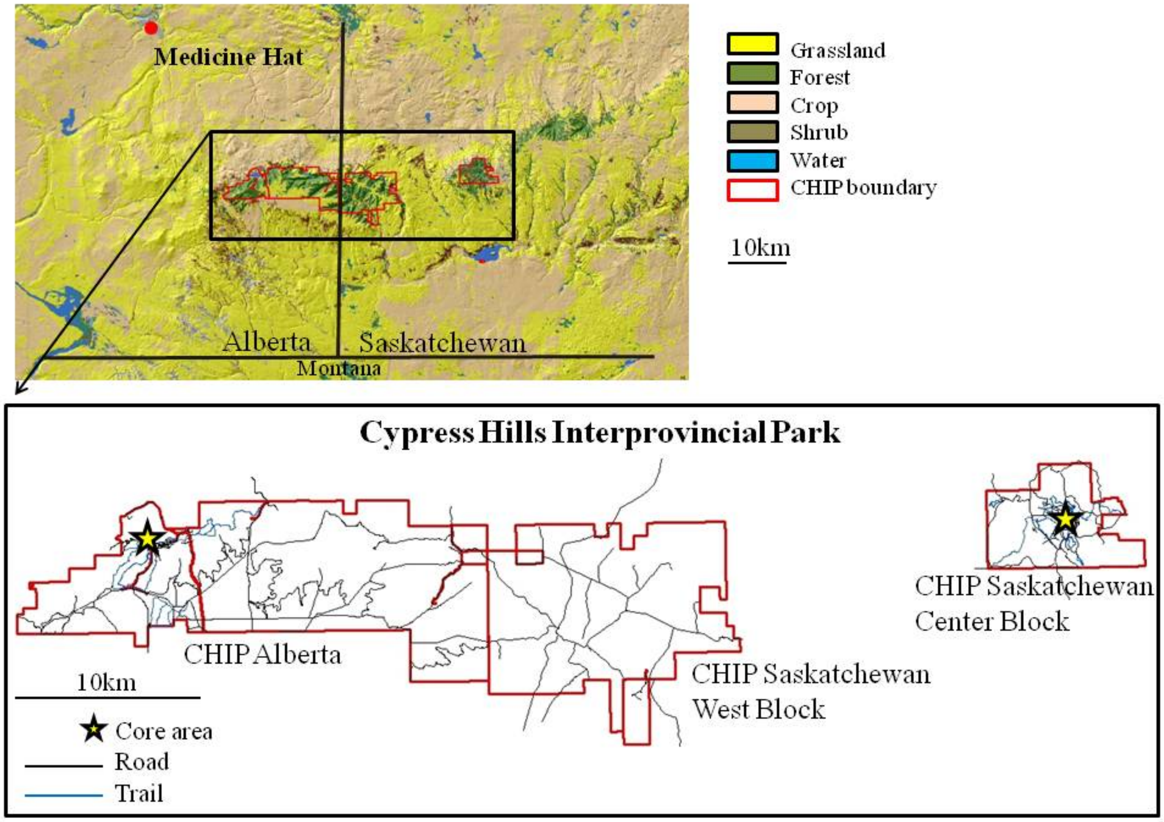

Figure 2.1: Study area: Cypress Hills Interprovincial Park (400 km^2) located in southeast Alberta and southwest Saskatchewan. Two core areas and an extensive network of roads and trails exist in the park to service visitors.

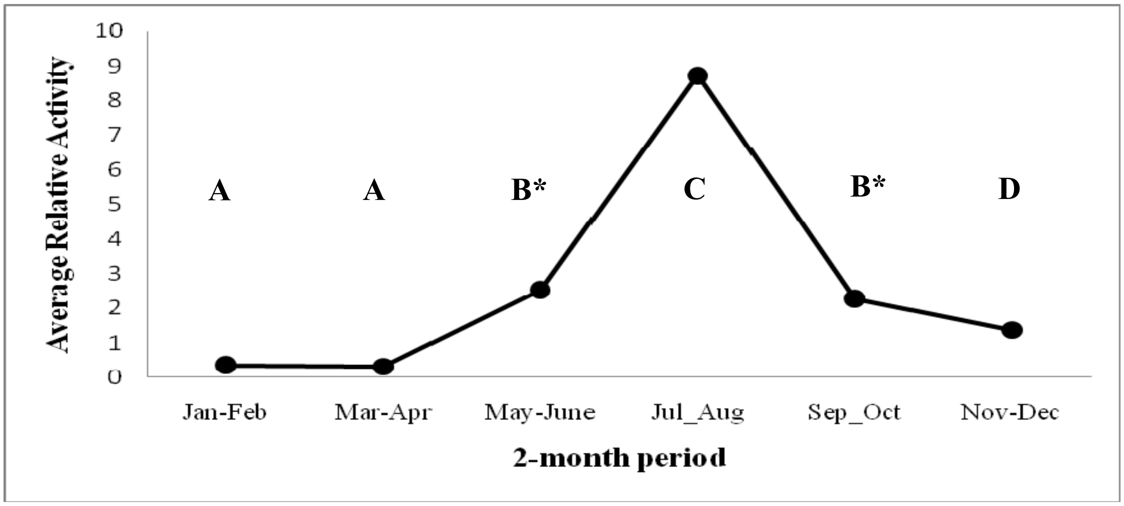

Figure 2.2: Average human activity (motorized and non-motorized combined) detected at camera locations in Cypress Hills Interprovincial Park, 1 July 2011 – 30 June 2012. Average human activity is reported here as real data but was natural-log transformed for statistical analysis. Letters indicate no significant differences between 2-month seasons based on pair-wise Wilcoxon tests using a Bonferonni corrected *P*-value = 0.003 for multiple comparisons. Periods that did not differ significantly were pooled into one season for modelling motorized and non-motorized human activity and cougar habitat selection. *Not pooled into one season to control for considerable environmental differences.

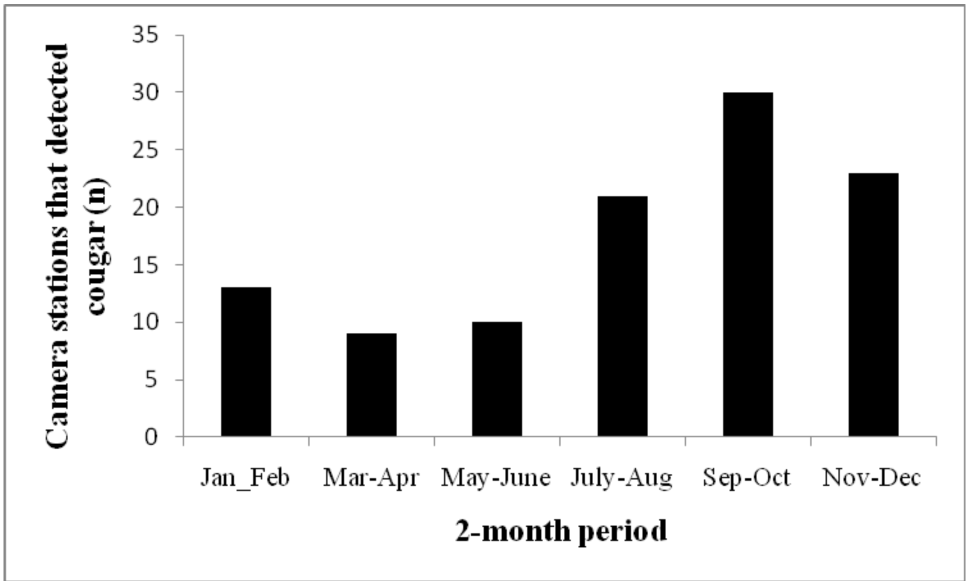

Figure 2.3: Number of camera stations that detected a cougar in each 2-month sampling period. Cameras were placed randomly along roads and trails in Cypress Hills Interprovincial Park and monitored from 1 July 2011 – 30 June 2012. Only cameras that were operational for all 2-month periods (*n*=61) were included in the analysis to ensure equal detectability.

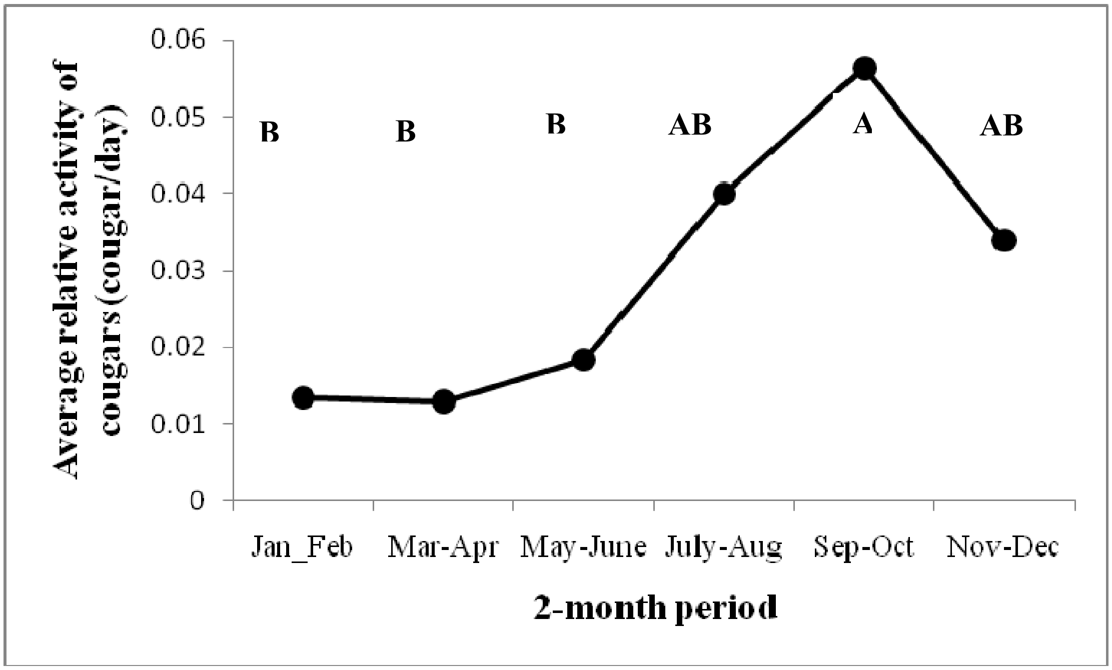

Figure 2.4: Average relative activity of cougars detected at camera locations in Cypress Hills Interprovincial Park, 1 July 2011 – 30 June 2012. Letters indicate no significant difference based on pair-wise Wilcoxon tests using a Bonferonni corrected *P*-value = 0.003 for multiple comparisons.

Table 2.1: Names and descriptions of candidate variables used to model seasonal motorized and non-motorized relative human activity in Cypress Hills Interprovincial Park.

Covariates	**Description**
dist_camp[a]	Distance to nearest campground
dist_core[a]	Distance to nearest core area measured from visitor centers
dist _park[a]	Distance to nearest parking
dist _entr[a]	Distance to nearest entry gate
dist _mentr[a]	Distance to nearest main entry gate
dist _sentr[a]	Distance to nearest secondary entry gate
dist _trailh[a]	Distance to nearest trailhead
dist _fclty[a]	Distance to nearest facility which included campground, core area, parking and entry gates
prox_core	Euclidean distance to core area
smmr_main[a]	Distance to nearest junction with main road
wntr_main[a]	Distance to nearest junction with winter main road
ski	Binary variable indicating if trail was maintained for xc-skiing
sled	Binary variable indicating if snowmobiling was permitted on trail
trail_type	Categorical variable for trail types excluding winter and summer main roads. Secondary roads was used as a reference category.

[a] calculated as distance along the trail using Network Analyst in ArcGIS10.

Table 2.2: Names and descriptions of variables used in candidate cougar resource selection function models.

Variables	Description
Environmental	
tri	Topographic roughness index (Jenness, J. 2012. DEM Surface Tools for ArcGIS); 90m resolution
cover	Binary variable indicating forest cover (1; conifer, deciduous, mixed forests and shrub) or open cover (0; grassland, cropland, exposed land); 30m resolution.
edg_inopn	Distance to edge for points in open
edg_infrst	Distance to edge for points in forest
dist_water	Distance to nearest water course
Anthroprogenic	
dist_trail	Euclidean distance to nearest trail
*MRA**	Estimated motorized relative activity of nearest trail from human MRA models
*NMRA**	Estimated non-motorized relative activity of nearest trail from human NMRA models

* Estimate changed by season according to seasonal human use model

Table 2.3: Candidate cougar habitat models and corresponding composite AIC weights (AICw_i) in each season. Composite AICw_i were calculated by averaging AICw_i of the individually-fit models in each season. *Combined_RA* (bold) ranked highest in AICw_i across all seasons and was used for population-level modelling. See Table 2.2 for descriptions of covariates.

		Composite AICw_i by season				
Model name	**Model structure**	**Winter**	**Spring**	**Summer**	**Fall**	**Hunt**
Enviro	*tri + cover + edg_inopn + edg_infrst+dist_water*	0.04	0.00	0.00	0.01	0.00
Trail	(*Enviro*) + *dist_trail*	0.02	0.01	0.09	0.06	0.05
Motor_RA	(*Trail*) + *MRA*	0.06	0.15	0.21	0.28	0.14
Non-motor_RA	(*Trail*) + *NMRA*	0.25	0.08	0.10	0.23	0.32
Combined_RA	**(*Trail*) + *MRA* + *NMRA***	**0.63**	**0.76**	**0.59**	**0.43**	**0.49**

Table 2.4: Summary of human activity by season in Cypress Hills Interprovincial Park, 1 July 11 – 30 June 12. Average overall relative activity (ORA), motorized relative activity (MRA) and non-motorized relative activity (NMRA) are reported here as real data for ease of interpretation. Human activity data was natural log transformed for statistical analysis. Average human activity rates are measured as people or vehicles per day.

Period	Avg trap days	Sum Motorized	Sum Non-motorized	Sum Total	Proportion of annual use	Avg ORA	Avg MRA	Avg NMRA
Jan-Feb	19.98	352	337	703	0.02	0.36	0.16	0.19
Mar-Apr	19.10	343	336	679	0.02	0.32	0.11	0.20
May-Jun	17.05	2161	1883	4044	0.14	2.53	0.99	1.51
Jul-Aug	19.52	10204	6625	16830	0.58	8.72	4.93	3.84
Sep-Oct	20.17	2728	1557	4285	0.15	2.27	1.12	0.25
Nov-Dec	19.78	2020	436	2456	0.08	1.37	1.30	0.96

Table 2.5: Most-supported seasonal models, based on AIC, estimating natural log transformed motorized and non-motorized human relative activity in Cypress Hills Interprovincial Park. See Table 2.1 for descriptions of model covariates.

Season	**Type**	**Winning model**
Winter	Motorized	*trail_type+dist_core+dist_entr+dist_park*
	Non-motorized	*trail_type+dist_core+ski*
Spring	Motorized	*trail_type*trailh*
	Non-motorized	*trail_type+dist_fclty+dist_entr*
Summer	Motorized	*trail_type+dist_fclty+dist_entr*
	Non-motorized	*trail_type+dist_entr+dist_core+dist_park+trail_type*dist_core+trail_type*dist_mpark*
Fall	Motorized	*trail_type*dist_core*
	Non-motorized	*trail_type*smmrmain*
Hunt	Motorized	*trail_type+dist_core*
	Non-motorized	*trail_type+dist_core+ski*

Table 2.6: Sample size of cougars and average number of GPS relocations that contributed to seasonal resource selection function models. Cougars were monitored between 2008 and 2012.

		GPS locations		
Season	**Sample size**	**Average**	**Min**	**Max**
winter	11	304	59	710
spring	11	281	82	494
summer	8	235	57	376
fall	6	260	79	467
late-fall	7	241	104	515

Table 2.7: A) Population-level coefficients for most-supported seasonal models based on AIC weights (Table 2.3). Population coefficients were calculated by averaging individual-level betas for each model respectively. Double asterisks (**) and single asterisks (*) indicates 95% and 85% confidence levels do not overlap zero, respectively. B) Direction of selection and significance for individual cougars. See Table 2.2 for variable names and descriptions.

A)

	Population-level Coefficients by Season				
Covariate	**Winter**	**Spring**	**Summer**	**Fall**	**Late-Fall**
tri	40.40**	13.16	38.40**	37.59**	30.75**
cover	0.52**	0.16	0.10	0.28	-0.36
edg_inopn	-0.008**	-0.009**	-0.006**	-0.003**	-0.02*
edg_infrst	-0.0005	-0.001**	-0.00009	-0.002	-0.003**
dist_water	-0.001**	-0.00002	0.00002	0.0004**	-0.0009**
dist_trail	-0.0007**	-0.0001	0.0005*	0.0002	-0.0003
NMRA	-0.26	-0.96**	-0.93*	-0.12	-6.50
MRA	-1.77	-0.43*	-0.10	-0.52	-0.03

B)

	Individual-level Selection by Season														
Covariate	**Winter**			**Spring**			**Summer**			**Fall**			**Late-Fall**		
	+	-	NS	+	-	NS	+	-	NS	+	-	NS	+	-	NS
tri	10	0	1	8	1	2	6	0	2	5	0	1	5	2	0
cover	6	2	3	5	2	4	2	3	3	3	0	3	3	2	2
edg_inopn	0	7	4	0	8	3	0	6	2	0	4	2	0	7	0
edg_infrst	2	4	5	1	5	5	2	5	1	1	4	1	1	5	1
dist_water	0	10	1	6	4	1	3	1	4	2	0	4	1	5	1
dist_trail	1	6	4	5	4	2	6	2	0	4	1	1	1	3	3
NMRA	4	3	4	2	8	1	1	5	2	2	1	3	1	1	5
MRA	5	6	0	3	6	2	2	2	4	1	2	3	3	2	2

Table 2.8: Day-period selection ratios of cougar use of the roads and trails in Cypress Hills Interprovincial Park calculated for each 2-month period. Use data was obtained using a network of remote cameras from 1 July 2011 – 30 June 2012. Expected use was based on the proportional duration of each day-period calculated at the mid-point of each 2-month sampling period.

	Selection Ratios			
	Morning	**Day**	**Evening**	**Night**
Jan-Feb	0.71	0.66	2.13	1.05
Mar-Apr	0.98	0.60	1.97	1.26
May-Jun	1.12	0.43	2.26	1.90
Jul-Aug	0.66	0.44	1.66	2.13
Sep-Oct	1.76	0.45	2.27	1.09
Nov-Dec	0.38	0.69	1.92	1.10
Seasonal Avg	0.94	0.55	2.03	1.42

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CHAPTER 3

SPACE-USE, MOVEMENT AND DISPERSAL OF SUB-ADULT COUGARS IN A GEOGRAPHICALLY ISOLATED POPULATION

INTRODUCTION

Cougars (*Puma concolor*) historically occurred across much of North America but were extirpated from large portions of their eastern range by direct persecution and reduced abundance of prey (Sunquist and Sunquist 2002). A significant increase in cougar occurrences throughout the Midwest in the past two decades indicates cougars are re-colonizing portions of their former range and expanding their distribution eastward (LaRue et al. 2012). Indeed, isolated breeding populations of cougars are confirmed in areas east of their contemporary range where there has not been an ecologically significant population of cougars in the past century. These areas are the North Dakota Badlands, the Black Hills in South Dakota, western Nebraska and the Cypress Hills spanning the Alberta-Saskatchewan border (Cougar Network 2007, Larue et al. 2012). The presence of wild cougars also has been confirmed recently in Ontario (Rosatte 2011) and Manitoba (Watkins 2005) but the source of these cougars and the population status in these provinces remain unclear.

This eastward range expansion can be explained by several factors including a shift towards conservation-based cougar management, an increase in deer abundance throughout midwestern North America (Cougar Management Guidelines Working Group 2005), the cougars' adaptability to moderate levels of human activity (Morrison 2013), and perhaps most importantly, their dispersal ecology (Thompson and Jenks 2005, LaRue et al. 2012). A recent study of cougar confirmations in the Midwest found that 76% of recovered carcasses were males (sex class typically associated with dispersal) and that cougar confirmations declined as distance from western source populations increased (LaRue et al. 2012). Furthermore, several sub-adult cougars have been observed dispersing from the Black Hills into the Midwest region and other unmarked individuals have been linked back to this isolated population (Cougar Network 2007, Thompson & Jenks 2010). These findings lend support to the hypothesis that dispersal is facilitating cougar range expansion which may be unfolding via a stepping-stone process (LaRue et al. 2012).

Dispersal in cougars has been described as the species' most dramatic phenomenon (Quigly and Hornocker 2010). Mechanisms driving cougar dispersal are not well understood but reducing competition for mates, reducing competition for resources, and avoiding inbreeding have been hypothesized as proximal factors (Logan and Sweanor 2001, Thompson and Jenks 2010). Cougars exhibit sex-biased dispersal; almost all males disperse while approximately 50% of sub-adult females remain philopatric (Logan and Sweanor 2001). Sweanor et al. (2000) describe the onset of dispersal as the departure from the cougar's natal range which occurs at an average age of 15 months. Congruent with differential dispersal behaviour, males typically disperse greater distances than females often covering several hundred kilometres (Sweanor and Logan 2010). Instances of extreme long-distance dispersals exceeding 1,000 km have been documented for both sexes (female: 1,341 km [Stoner et al. 2008], male: 1,067 km straight-line [Thompson and Jenks 2005]).

During dispersal, cougar movements are characterized by fast-paced directional bouts broken up by a series of temporary or transient home ranges (THRs; Beier 1995, Sweanor et al. 2000, Stoner et al. 2008). These localizing events may be an important component of dispersal during which cougars evaluate competition for resources and mates. Therefore THRs may represent aborted attempts to establish a permanent home range (Stoner et al. 2008). Dispersing cougars have been documented using habitats ideally suited to the biology of the species (i.e., providing cover and prey) but also have used fast-paced movements (Sweanor et al. 2000) and corridors (Beier 1995) to cross matrices of relatively unsuitable habitat. Without the presence of adequate corridors, dispersal by panthers in Florida was impeded by anthropogenic landscape features that eventually led to juvenile cougars, including males, returning to the vicinity of their natal ranges (Maehr et al. 2002). Flat open expanses also have proved to be sufficient barriers to movement capable of limiting gene flow among populations (McRea et al. 2005) and cougars have been documented to select against grasslands, agriculture and pasturelands (Laing 1988, Dickson et al. 2005), which are dominant cover types in the Midwest (LaRue and Nielsen 2008).

If cougars continue to re-colonize the grassland-dominated landscape of the Midwest, their distribution will likely be spatially structured as isolated sub-populations separated by a matrix of less-suitable habitats. Dispersal is fundamental to re-colonize vacant habitat patches and maintain the long-term presence and genetic viability of isolated populations (Sweanor et al. 2000, Quigley and Hornocker 2010). As such, understanding how cougars traverse the Midwest matrix and how re-established populations can serve as stepping stones for continued range expansion and gene-flow among isolated populations will be important for cougar conservation at a landscape-level. However, little is known regarding cougar dispersal in the Midwest in part because the phenomenon is relatively recent and also because far-ranging animals have been difficult to track with past radio-telemetry technologies.

Until recently it has been cost-prohibitive to fit juvenile cougars, especially males, with GPS collars because of the high likelihood the cougars would disperse and be lost to the study. Instead, VHF collars were often deployed providing coarse spatial and temporal data. Often dispersal data were collected once per week (Beier 1995, Thompson and Jenks 2010) or opportunistically if cougars were located by other means such as human-caused mortality, camera traps or genetic samples (Thompson and Jenks 2005, Cougar Network 2007, LaRue et al. 2012). As a result, the limited amount of research on cougar dispersal in the Midwest has focused primarily on coarse scales of movement such as the direction and straight-line distance travelled (Thompson and Jenks 2005, Thompson and Jenks 2010). Due to the lack of fine-scale empirical data on cougar spatial ecology in this region, researchers have relied on expert opinion (LaRue et al. 2012) and isotopic clues (Henaux et al. 2011) to estimate potential dispersal corridors.

Recent advances in satellite-GPS collar telemetry improve our ability to track animals over long distances by transmitting spatial data via satellite to email. This has facilitated fine-scale analysis of movements and habitat selection by transient animals. Using this technology, my objective was to obtain a fine-scale quantitative assessment of sub-adult space-use and movement in the Cypress Hills to examine factors influencing dispersal ecology in an isolated population. I first characterize and quantify sub-adult ranging behaviour including movement parameters and the spatial distribution of temporary home ranges in relation to known adult range. Second, I assess fine-scale habitat use and selection during transience and localizing behaviours. Lastly I quantify factors influencing cougar movement rates during sub-adult life.

STUDY AREA

The Cypress Hills (Fig. 1) are an insular formation of foothills, located in southeastern Alberta and southwestern Saskatchewan, which rise several hundred meters above the surrounding landscape. The hills are distinguished from their surroundings by their abundance of tree cover consisting primarily of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*). The matrix surrounding the hills is an expanse of mixed grasslands, pasture lands and agriculture development characteristic of much of midwestern North America (LaRue and Nielsen 2008). The Cypress Hills' high elevation (1,234 m, Elkwater, AB) results in cooler summers and warmer winters than the surrounding lowlands. The average temperature is 19.1 C in July and -3.3 C in

January. Annual precipitation is 533.5 mm which is greater than the surrounding area.

The closest known breeding populations of cougars are 200 km south in the Bear Paw Mountains in Montana and 250 km west in the Rocky Mountains of southwestern Alberta. The primary diet of cougars in the Cypress Hills is white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), porcupines (*Erethizon dorsatum*) and elk (*Cervus canadensis*) (Bacon et al. 2011, Morrison unpublished data).

METHODS

Cougar capture and collaring

Sub-adult cougars were captured in the Cypress Hills during 2010 and 2011 with the assistance of a professional houndsmen and trained tracking hounds. All animal handling was done by trained personnel in accordance with Animal Use Protocol 568-02-11 approved by the University of Alberta Animal Care Committee. All male cougars were fitted with Argos- (Lotek 4400s) or Iridium-based (Advanced Telemetry Systems) satellite-GPS collars that transmitted the data to an email receiver every 2-6 days. Females were fitted with either a satellite-GPS collar or a standard GPS collar (Lotek 4400s) that required downloading the data remotely with a hand-held command unit. All collars were programmed to take a fix every 3 hrs. For reference, cougars were coded by their sex and the order in which they were captured in relation to all other cougars captured for this study (e.g., F1=first female).

Characterizing sub-adult ranging behaviour

Cougar GPS data were analyzed from the first independent foray away from the cougar's natal range until the onset of adulthood (36 months or evidence of breeding), the cougar's death, the loss of the GPS-radio collar, or the end of the study. During this period, sub-adult GPS relocations were categorized into two ranging behaviours: transience and localizing. Transience was characterized by unidirectional movements, often into novel terrain, and included true dispersal events, where the animal never returned, and exploratory forays, where the cougar ultimately returned to its natal home range or a previous temporary home range (THR). Localizing was characterized by a cougar ceasing unidirectional movements and demonstrating site attachment to an area for at least 20 days. All localizing bouts were considered a THR since the potential existed that the site would later be abandoned. This localizing behaviour was no longer considered a THR at the first evidence of breeding or if a cougar localized for more than 12 months.

Temporary home ranges were delineated using a 95% kernel density estimate. I calculated the area (km^2) of each THR and the straight-line and cumulative distances travelled from the center-point of the last THR to the center-point of that cougar's natal home range. Percent overlap of each THR with known occupied adult range was calculated to examine the spatial distribution of sub-adult THRs in relation to adults. Adult range was based on the aggregated distribution of GPS locations from 9 adult cougars (2 males, 7 females) monitored between 2008 and 2013 (Bacon 2010, Morrison unpublished data). GPS locations for adults exhibited fidelity to the three distinct habitat patches that comprise the Cypress Hills. Based on this sample, and supported by field observations, I make the assumption that these patches are primary habitats and that adult densities are considerably higher in these patches than in the surrounding matrix. Habitat quality of sub-adult male and female THRs was quantified by calculating the average proportional composition of six primary cover types (shrub, wetland, grassland, agriculture, pasture and treed) in THRs for each sex class and comparing these composition values with that of aggregated adult range. Finally each sub-adult cougar was classified as a disperser or philopatric if their last known home range (THR or established) overlapped with their natal range by <5%, or >5%, respectively (Sweanor et al. 2000).

Habitat use and selection

Both habitat use and habitat selection provide important context to the spatial ecology of a species. I first quantified habitat use during transience and localizing by calculating the average proportional composition of cover types in localities used by individual cougars based on telemetry relocations. I quantified habitat selection by estimating resource selection functions (RSF) to identify landscape attributes selected by sub-adult cougars during transience and localizing behaviours. RSFs were estimated using conditional logistic regression to quantify the relative probability of a site being selected (Manly et al. 2002, Boyce et al. 2003). I used conditional logistic regression to pair one observed location with multiple random locations within an ecologically relevant extent (Compton et al. 2002, Boyce et al. 2003, Whittington et al. 2011). For species or individuals without well-defined home ranges, as is the case with sub-adult cougars, the conditional logistic design more accurately reflects the choices made during habitat selection (Compton et al. 2002) compared to sampling availability at home range scales (level II & III, Johnson 1980). Hence, each GPS location was buffered by 2000 m, which approximated the 90th percentile of observed 3-hr step lengths of sub-adult cougars, and 10 random points were generated within each buffer to sample availability.

I used a two-stage modelling approach whereby coefficients are first estimated for individual cougars and then averaged to obtain a population-level estimate (Nielsen et al. 2002, Sawyer et al. 2006, Fieberg et al. 2010). This method treats the individual animal as the sampling unit, instead of the GPS relocation, alleviating concerns regarding autocorrelation often associated with spatio-temporal data. Models of habitat selection by individual cougars were chosen on the combination of covariates that resulted in the lowest Akaike's Information Criterion (AIC; Burnham and Anderson 2002). In cases where a covariate was not included in an individual model, it received a beta value of 0 when calculating the population-level model. Due to the small number of GPS relocations during dispersal for two females (F1 & F5), data for these two individuals were combined and a single model was estimated. Due to the limited number of cougars monitored, males and females were pooled when calculating population-level models.

Candidate landscape variables were chosen based on characteristics deemed important to the biology of the species. These included topographic roughness (*TRI*), elevation (*elevation*), distance to hydrological features (*hydro*), distance to open water (*water*), distance to paved (*pavd_rd*) and unpaved roads (*unpavd_rd*), and land cover (*cover*). Quadratic terms were included for all continuous variables to assess non-linearity. Continuous variables also were tested for collinearity using a threshold Pearson correlation coefficient of $|r|=0.7$, above which the two correlated variables were restricted from entering the same model. Land cover was a categorical variable obtained from Land Cover for the Northern Sagebrush Steppe Initiative Area (30m resolution; NSSI; Montana Fish Wildlife and Parks 2011). Land cover was condensed into 6 primary cover types which were *shrub, wetland, grassland, agriculture, pasture* and *tree*. Tree cover included deciduous, conifer and mixed woods and was used as a reference category in the models because of its established importance for cougars and because I was interested in examining selection related to more open habitat types. Other land cover classes identified by NSSI but not included in the 6 primary categories were accounted for by other habitat covariates (e.g., *water*) or were masked from being sampled because they comprised a small fraction of habitat types available and were rarely, or never, encountered by cougars during this study. All covariates were standardized for statistical analysis.

Movement

In addition to assessing the habitat characteristics that influenced cougar space-use, I also examined how these landscape variables affected cougar movements. Step length, defined as the distance between consecutive GPS relocations (Turchin 1998), is a measure of speed that can be used to quantify cougar response to multiple habitat variables. Linear regression was used to estimate a population-level movement model using the same two-staged approach described for the habitat-selection models. Step length was right skewed so a natural log transformation was performed prior to statistical analysis. Only steps that linked two consecutive fixes were included in the analysis to ensure all steps were equal in duration.

Candidate explanatory variables in the step-length model included all the same covariates available in the RSF models but used unit measures appropriate for linear sampling units. More specifically, for each step I calculated the length-weighted mean for topographic roughness, elevation, distance to hydrological features, distance to open water, and distance to paved and unpaved roads. To characterize cover types I calculated the proportional composition of each cover type that a step intersected. To eliminate potential issues of collinearity associated with proportional composition (i.e., all proportions sum to 1) I excluded tree cover from the model to serve as a reference category for land cover. All covariates were standardized for statistical analysis.

In addition to habitat covariates, day-period was included as a categorical variable by binning GPS relocations into day (fixes obtained at 900, 1200 and 1500 hrs), crepuscular (600 and 1800 hrs), and night (0300, 2100 and 2400 hrs). Also, instead of estimating separate models for transience and localizing, I included ranging behaviour as a categorical variable (*ranging*) to test whether cougars moved faster during transience while accounting for the effects of other habitat characteristics. Finally I included interaction terms to test for diel shifts in activity associated with land cover or ranging behaviour.

RESULTS

Cougar captures and GPS data

In total, 7 juvenile cougars, including 4 males (M3, M7, M9, M10) and 3 females (F1, F4, F5) were fitted with GPS-radio collars. Six cougars were initially collared while still dependent on their mothers. The remaining cougar (F1) was collared as an independent juvenile and was estimated to be 18 months at time of capture. After independence, sub-adult cougars were monitored for an average of 240 days (min=88, max=411) during which an average of 1,481 GPS relocations (min=385, max=2,694) were collected per individual.

Characterizing sub-adult ranging behaviour

All sub-adult cougars displayed movement bouts characteristic of transience and localizing. During transience, 6 cougars made exploratory forays into the surrounding grassland-dominated matrix. However, all but one cougar (M10) eventually returned to the vicinity of the Cypress Hills. I delineated 7 THRs used by males and 4 THRs used by females (Table 3.1). The average female THR was 72.58 km^2 and overlapped with adult range by 79.80%. Male THRs averaged 172 km^2 with 16.07% overlap of adult range. Average land-cover composition used by male THR's included significantly more grassland ($P < 0.05$) and significantly less forested cover ($P < 0.05$) than sub-adult females.

Otherwise there was no significant difference (*P* > 0.05) observed between male and female THRs in the remaining land cover categories (Fig. 3.2). Overall, average female THRs more closely approximated the composition of adult range than did male THRs (Fig. 3.2). Average distance from the center point of the last THR to the center point of their natal range was 13.71 km for females and 165.30 km for males. Average cumulative distance covered during transience was 132.10 km for females and 364.27 km for males (Table 3.1). Cougar F5 remained philopatric to her natal range while cougar F4 dispersed. A third female (F1) was captured post independence so no conclusions can be made in regards to her natal range. All four male cougars dispersed from their natal ranges. One male (M10) dispersed from the study area completely and traversed 749.28 km (487.66 km straight-line distance) covering portions of northeast Montana and much of southern Saskatchewan before establishing his first THR near Moose Mountain Provincial Park in southeast Saskatchewan (Fig. 3.3).

Habitat use and selection

During transience and localizing cougars used all 6 land cover types available (Fig. 3.4). Forest cover comprised the greatest proportional use during both ranging behaviours, followed by grassland, agriculture and then shrubland (Fig. 3.4). At the population level, cougars selected rough terrain and proximity to hydrological features during both ranging behaviours (Table 3.2). Regression coefficients for elevation were negative during both ranging behaviours (Table 3.2) but with a markedly steeper slope during transience (Fig. 3.5). Proximity to roads had an insignificant effect on cougar habitat selection during transience but cougars avoided areas in close proximity to paved and unpaved roads while localizing in THRs (Table 3.2). This avoidance became less pronounced as distance to both road types increased (Fig. 3.5). Response to paved roads was non-linear and the relative probability of selection began to decrease when distance to paved roads exceeded approximately 12.5 km (Fig. 3.5). Distance to open water had little effect on habitat selection during transience but cougars showed a weak and non-linear response while localizing (Table 3.2, Fig. 3.5). Relative to tree cover, cougars had negative selection coefficients for all land cover classes during both ranging behaviours (Table 3.2). This negative selection was greatest for agriculture followed by grasslands and then pasturelands. Selection was not significant for wetlands during transience and shrubland while localizing.

Movement

I analyzed an average of 1,344 steps per sub-adult cougar (min=261, max=2,309). The final population-level model included all candidate covariates but not all were significant predictors of step length (Table 3.3). Length-weighted means for elevation, proximity to paved roads and proximity to open water did not appear to influence cougar step length (Table 3.3). Cougar step length initially increased as the length-weighted means for distance to unpaved roads and distance to hydrological features increased but eventually began to decrease as length-weighted means to these features became exceedingly large (Fig. 3.6). Cougar movements slowed as topographic roughness increased (Table 3.3, Fig. 3.6).

Proportion of shrubland and wetland did not influence cougar step length in relation to proportion of tree cover (Table 3.3). However cougar step length increased in grasslands, agriculture and pasturelands and this pace quickened significantly at night through these open habitats (Table 3.3, Fig. 3.6). Cougars also moved shorter distances at night during localizing than during transience, relative to crepuscular periods but there was no difference detected between day time step lengths during the two ranging behaviours (Table 3.3).

DISCUSSION

My results support many aspects of our current understanding of sub-adult cougar ecology but provide important insights into their space-use and movements in a recently re-established populations occurring in isolation east of contemporary range.

Characterizing sub-adult ranging behaviour

On average, the total distance traversed by males was greater than by females, which is congruent with sex-biased dispersal behaviour observed in other cougar studies (Sweanor et al. 2000, Thompson and Jenks 2010, Maehr et al. 2002). As expected the total distances covered during dispersal were far greater than the straight-line distances from the cougar's natal range to its last known location. Stoner et al. (2008) observed a similar discrepancy in measures of displacement for an exceptional young female that travelled 1,341 km during dispersal but was relocated only 357 km from her point of first capture. While past studies have relied on straight-line distances to quantify dispersal movements

(Sweanor et al. 2000, Thompson and Jenks 2010), my findings exemplify how our understanding of juvenile-cougar spatial ecology stands to improve with advancements in GPS-radio collar technology.

By collecting fine-scale spatial and temporal data I documented several instances of cougars travelling greater than 200 km during transience. The most notable dispersal event was that of cougar M10 who successfully traversed 749 km over 100 days, from 13 February 2012 to 22 May 2012. Cougar M10 maintained fast-paced directional movements throughout this dispersal until he arrived in the vicinity of Moose Mountain Provincial Park – the first large suitable habitat patch he encountered. Here he localized for 27 days until his collar quit transmitting. Although there is no known breeding population of cougars in Moose Mountain, the presence of at least one other cougar was confirmed during winter 2012 with remote cameras (J. Karst, Saskatchewan Fish and Wildlife, 2012, personal communication). The presence of this unknown cougar provides one more confirmation that cougars are reaching isolated habitat patches several hundred kilometres from known source populations and M10's data provide one of the first fine-scale documentations of how these long-distance dispersals are accomplished.

Transience was characterized by juvenile cougars leaving their natal range and making directional fast-paced movements along the fringes of known adult range or into the surrounding grassland-dominated matrix. Sub-adult cougars in the isolated Black Hills also were observed moving to the periphery of primary habitat before dispersing from the study site or establishing home ranges

(Thompson and Jenks 2010). During transience 6 cougars made exploratory forays extending away from the Cypress Hills however all but M10 eventually returned to the vicinity of the Hills. Indeed large flat open expanses, such as agriculture, have been hypothesized to pose barriers to movement for cougars (McRea et al. 2005). None the less, the increase in cougar sightings throughout the Midwest coupled with this study's observations of short- and long-distance dispersals indicate this landscape is sufficiently permeable. Therefore sub-adult cougars emanating from these isolated populations are faced with a trade-off between the risks of dispersing long distances through less-suitable habitat or coping with increased environmental pressures (i.e., competition for resources/mates) that are hypothesized to drive dispersal (Logan and Sweanor 2001).

Ultimately all males successfully dispersed from their natal range which satisfies the inbreeding avoidance hypothesis of dispersal. One female dispersed from her natal range and one female returned to her natal range following a dispersal foray and remained philopatric. Although only one cougar successfully emigrate from the Cypress Hills region, the high rate of long-distance exploratory forays observed could indicate that environmental drivers are reaching threshold levels. Under the hypothesis that female dispersal is at least partially density dependent (Logan and Sweanor 2001), geographically isolated populations of cougars could be expected to produce a greater number of female dispersers in which case these populations will serve as important stepping stones promoting, and potentially expediting, re-colonization into suitable areas further east.

Thompson and Jenks (2010) hypothesize that the mate-procurement hypothesis is the leading mechanism driving long-distance dispersal in sub-adult males. Sub-adult males in the Cypress Hills, who did not ultimately disperse away from the study area, used THRs that overlapped minimally with adult range and had habitat compositions dominated by grasslands, a cover type that was less preferred to forested cover by both males and females alike (Fig. 2). The tendency for sub-adult males to localize in less-suitable habitats on the outskirts of adult range would limit direct competition with resident males. This was supported by observations of M3 that initially occupied a THR with 52% adult range overlap but rather suddenly re-localized to a THR with 20% overlap. During a recapture shortly after this shift in THRs, M3 showed signs of injuries indicative of conspecific strife including puncture wounds and scaring to his face, chest and hind leg. On the other hand, it is unclear how this avoidance strategy provides access to mating opportunities which is of equal importance to the mate procurement hypothesis. At the close of the study, three males were last observed using THRs adjacent to adult range; however one was killed by humans, one had only localized for less than a month, and all three were still considered sub-adults. Additional long-term monitoring would be required to examine if these satellite males could eventually compete with dominant males in order to recruit into the population or if they would be required to emigrate to seek breeding opportunities elsewhere, as was observed in the Black Hills (Thompsons and Jenks 2010).

Although only one female displayed philopatry, all females had considerable THR overlap with known adult range and had THR habitat composition which more closely approximated that of primary habitat. Two of the three females successfully established adult home ranges and showed evidence of breeding through the formation of GPS clusters indicative of denning. These data indicate sub-adult females were successfully recruited into the Cypress Hills population and were able to establish home ranges in prime cougar habitat. True range expansion is dictated by the presence of females (Thompson and Jenks 2010). As a result, male-biased dispersal patterns, in terms of distance and rates, still could be a major factor limiting the pace and extent of cougar range expansion and re-colonization.

Habitat use and selection

Relative to tree cover, sub-adult cougars showed strong selection against all other habitat types. Notably, this negative selection was greatest for agriculture, grasslands and pasturelands during both ranging behaviours. This is consistent with other studies that documented avoidance of these open habitats (Laing 1988, Dickson and Beier 2002). Although cougars selected against these cover types, cougars were still documented using all available cover types. The high proportional use of tree cover is a product of selection for this cover type while the use of grasslands, which ranked second in proportional use, reflects its relative abundance in the Cypress Hills study area and the greater Midwest region (LaRue and Nielsen 2008). The use of all cover types during both types of ranging behaviours highlights the adaptability of cougars to use a broad range of habitats and indicates these habitats offer some level of permeability which has obvious implications for facilitating cougar dispersal in the Midwest.

In response to terrain features, cougars demonstrated positive selection for areas with increased topographic ruggedness during both ranging behaviours. This fits our understanding of cougar habitat selection from other studies (Arundel et al. 2007). Cougars selected for lower elevations (i.e., higher relative probability of use at lower elevations) during both ranging behaviours but the slope of the response curves differed dramatically. Localizing cougars demonstrated a gradual response to elevation which could be explained by the sub-adult's tendencies, especially males, to avoid the forested uplands dominated by adult cougars. During transience the relative probability of use dropped quickly with increases in elevation. This indicates low lying features are likely important travel corridors for cougars during dispersal, perhaps providing some form of lateral cover to offset the lack of vegetative cover in more open habitat types. In California, cougars were observed using canyon bottoms as preferred travel routes (Dickson and Beier 2007).

Proximity to hydrological features also was a selected habitat characteristic during both ranging behaviours. These results support models by LaRue and Nielsen (2008) that predicted high stream densities within dispersal corridors consistent with other findings that cougars select for riparian areas (Dickson and Beier 2002). In many instances, hydrological features likely support riparian-type habitats not apparent at a land-cover resolution of 30 m but which provide fine-scale corridors for cougars. Historically cougars were documented along rivers and in riparian areas throughout the Midwest but land-use transformations over the past century might have affected the ability of these features to support populations or even to serve as corridors (Laundré 2012). For example, cougar M10 encountered the Milk River basin during his dispersal but only followed the river for approximately 46 km (or less than 7%) of his total observed dispersal distance. Had he followed this river system past its confluence with the Missouri River it would have brought him into close proximity to the cougar population in western North Dakota

Localizing sub-adult cougars had a non-linear response to distance to open water with the relative probability of selection maximized at approximately 2.8 km. In other studies, nearness to open water was a preferred habitat characteristic for cougars (Arundel et al. 2007) which explains why the relative probability of selection I observed decreased at greater distances. In the Cypress Hills however, many of the large open water sources are associated with high human recreation which justifies cougar avoidance of near-proximity to water. Maintaining some overall affinity to water while avoiding humans would result in the non-linear response I observed. Additionally, this result also might be partially explained by observations of juvenile cougars attempting to avoid competition with resident cougars, especially males. Indeed, Arundel et al. (2007) did document selection for proximity to water as strongest for male cougars. These two hypotheses (i.e., avoidance of humans and avoidance of competition) are not necessarily mutually exclusive. During transience, open water was not included in the most-supported individual model for any cougar and thus was not included in the population-level model. This apparent indifference makes sense because open water represents a localized resource that might be less important to a travelling cougar. Moreover, dispersing animals would be less prone to actively avoid close proximity to these features because they would likely not be associated with resident cougars and might have less human activity outside a Provincial Park setting.

During localizing behaviour cougars avoided areas in proximity to both paved and unpaved roads but appeared indifferent to these features during transience. Cougar response to roads and other human development is complex. Morrison (2013) documented diel and seasonal shifts in cougar space-use around roads and trails in response to fluctuating levels of human activity. Other studies have documented paved roads as barriers to movement (Sweanor et al. 2000, Arundel et al. 2007) while gravel roads served as movement corridors for cougars (Dickson et al. 2005, Kertson et al. 2011). Localizing cougars may become accustomed to human activity levels on roads within their THRs and adjust their space-use accordingly. During transience however, cougars moved greater distances at night and therefore were more likely to encounter roads when traffic levels are reduced. Indeed, cougars in southwest Alberta appeared ambivalent to roads at night that received <1 vehicle/hour (Banfield 2012). Although proximity to roads may not influence fine-scale cougar habitat selection during dispersal it logically increases the risk of human-caused mortality. As such, cougars would still benefit from corridors with lower road densities and human development (LaRue and Nielsen 2008).

Movement

In addition to analyzing space-use by sub-adult cougars, I quantified how landscape variables affected cougar movement. During both ranging behaviours, cougars moved greater distances during the night and shorter distances during the day compared to crepuscular periods. Cougars also moved significantly further at the night during transience than while localizing, indicating cougars were relying on the cover of darkness while traversing novel landscapes. Cougars also increased step length when traversing habitats dominated by grassland, agriculture and pastureland – cover types negatively selected by cougars – and moved greater distances in these less-preferred habitats during night and crepuscular periods than during the day. Again cougars appear to rely on darkness to provide cover while crossing relatively open habitats and moved faster through less preferred cover types.

Cougars also moved faster as topographic roughness decreased and as the overall proximity to hydrological features increased. Cougars selected for both rough terrain and proximity to hydrological features which lends further support to my findings that cougars increase their movement rates while traversing less desirable habitats. Dispersing cougars in a range and basin landscape in New Mexico also used fast-paced directional movements to cross matrices of unsuitable habitat (Sweanor et al. 2000). On the contrary, cougars slowed their movement as overall proximity to unpaved roads increased. Arundel et al. (2007) noted a similar decrease in movement rates and less angular movements when cougars were in proximity to highways and urban areas. My results support the hypothesis that cougars may respond differently to dynamic landscape variables, such as fluctuating activity levels on roads, by adopting more cautious slower-paced movements.

Management implications

In general, sub-adult cougars selected for similar habitat characteristics during transient and localizing behaviours with a few notable exceptions in response to roads, open water and elevation. Both ranging behaviours are likely important components of dispersal so it is expected that sub-adults would direct their movements and residency, when possible, in habitats most likely to meet the species' biological requirements. Transient behaviour quickly satisfies certain dispersal drivers, such an inbreeding avoidance, and likely reduces the potential for conflict with conspecifics. Localizing allows a more thorough assessment of resource availability and competition and can lead to an established home range or alternatively, THR abandonment in search of more favourable conditions.

By co-examining space-use and movement of sub-adult cougars in an isolated population my results provide insight into how cougar range expansion is progressing in the North American Midwest. Managers should realize that although certain habitat characteristics are preferred, cougars will not restrict their movements to these features. Instead cougars will adopt faster, nocturnal movements to effectively limit their residency and exposure in these less-suitable landscapes. In doing so, cougars can successfully disperse several hundred kilometres across grassland-dominated landscapes in search of resources and mates.

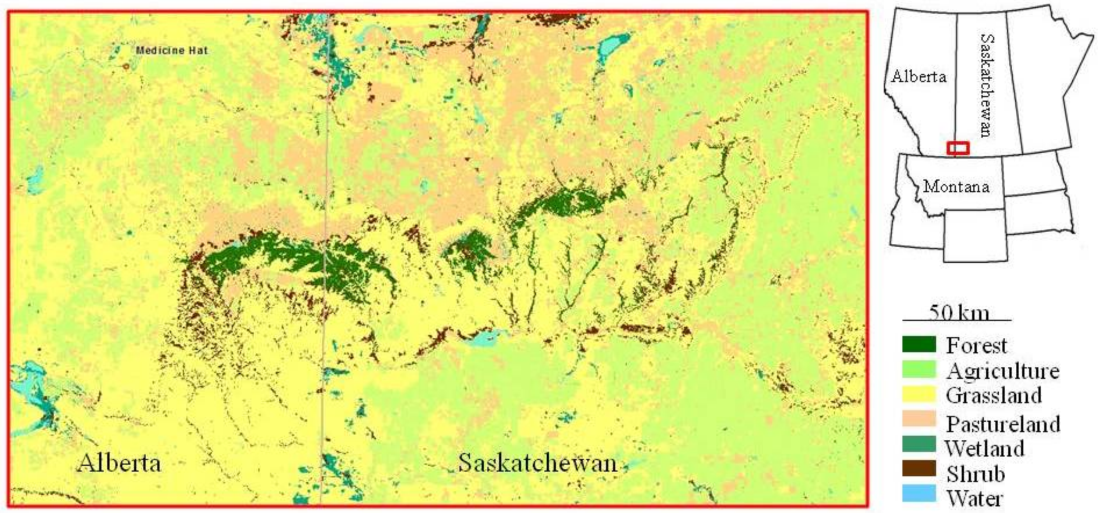

Figure 3.1: The Cypress Hills study area, located in southeast Alberta and southwest Saskatchewan. The geographic extent of the hills is distinguished by an abundance of forest cover. The matrix surrounding the hills is an expanse of mixed grasslands, pasture lands and agriculture development characteristic of much of Midwestern North America.

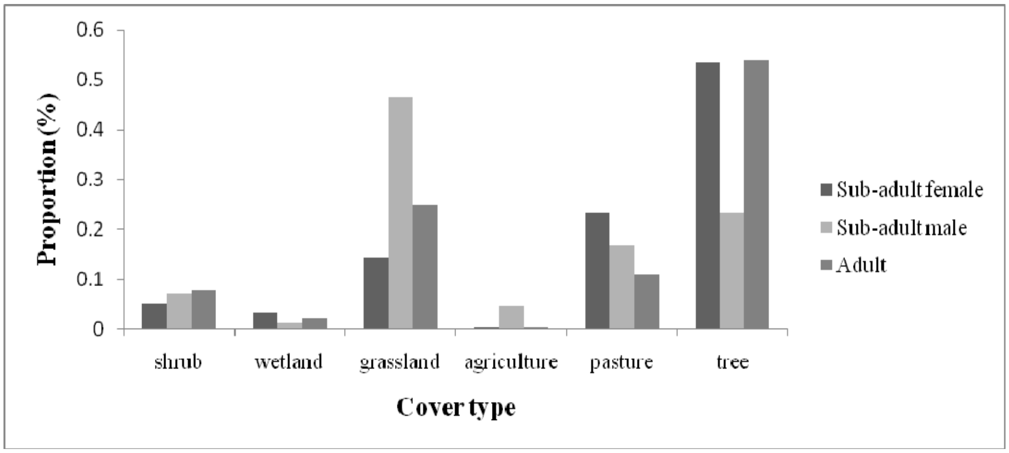

Figure 3.2: Average habitat composition of temporary home ranges of sub-adult males and females and of aggregated ranges of adults observed in the Cypress Hills, 2009-2012.

Figure 3.3: Dispersal route of a sub-adult male (cougar M10) who was fitted with a GPS-satellite collar in the Cypress Hills, Aug 2011. Cougar M10 covered 749.28 km over 100 days (13 Feb 2012 – 22 May 2012) before localizing in the vicinity of Moose Mountain Provincial Park in southeast Saskatchewan.

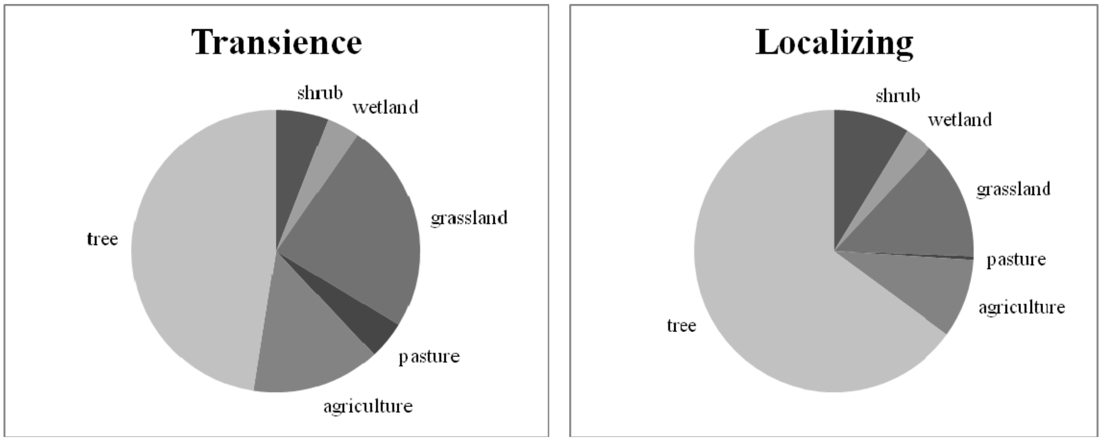

Figure 3.4: Average proportional use of primary land cover types by sub-adult cougars during transience and while localizing. Proportions were calculated for individual cougars based on the GPS relocations collected at three hour intervals and include any potential land-cover-related fix success bias. Sub-adult cougars were collared in the Cypress Hills and monitored between winter 2010 and summer 2012.

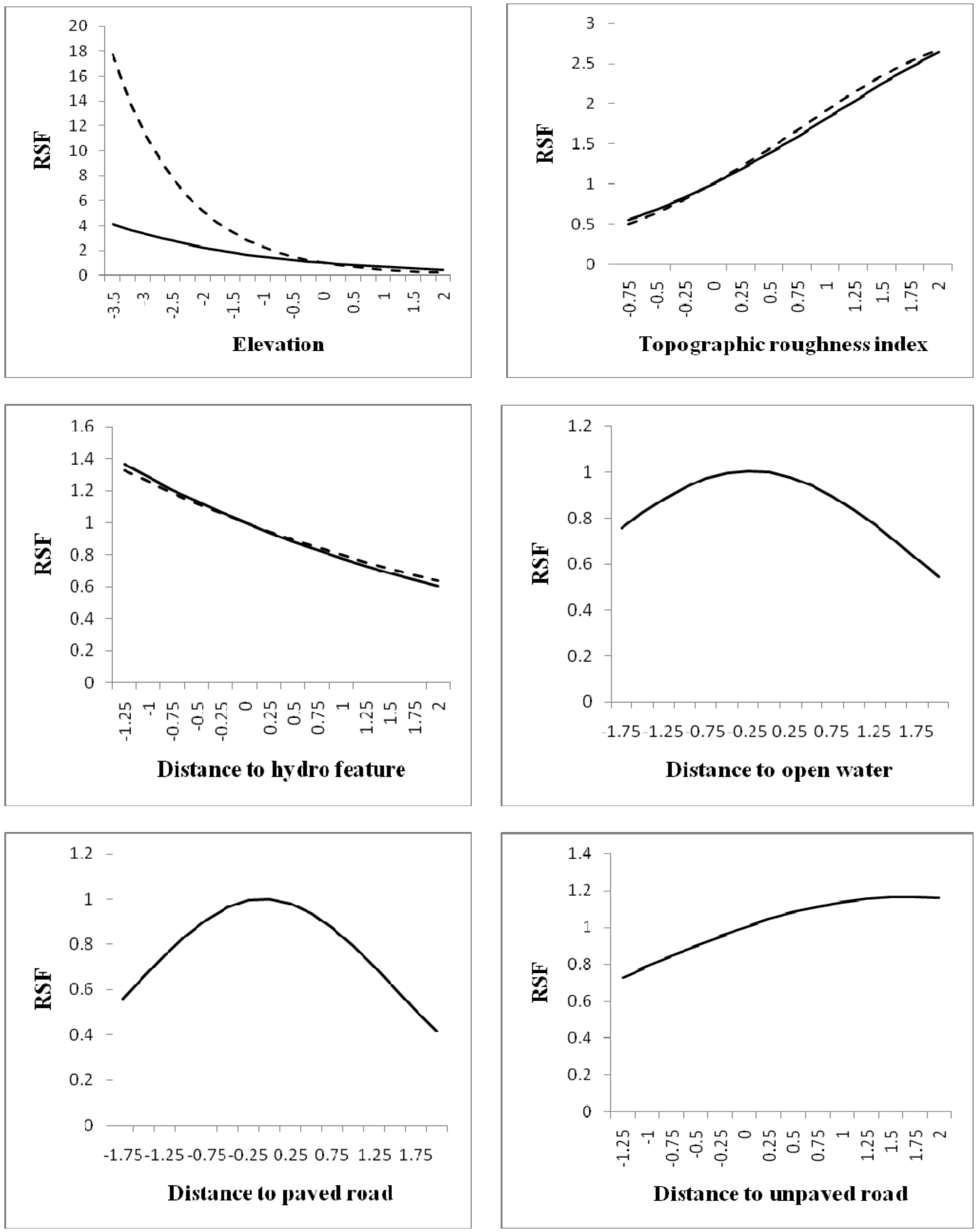

Figure 3.5: Resource selection functions (RSF) for sub-adult cougars in the Cypress Hills plotted over standardized range of habitat covariates. Response curves are plotted only for significant covariates in the Transient (dashed line) or Localizing (solid line) population-level models (see Table 3.2)

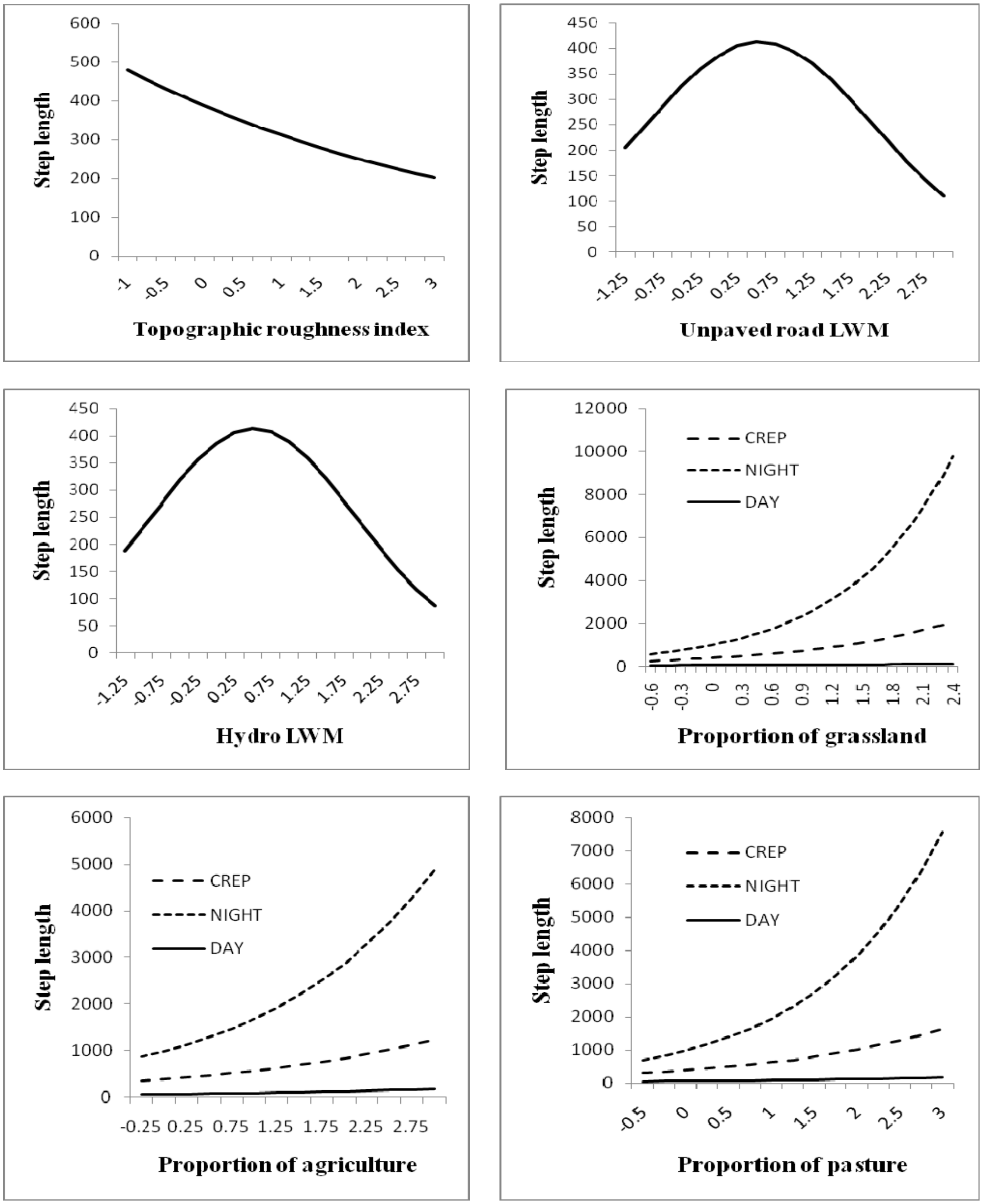

Figure 3.6: Step length estimates for sub-adult cougars in the Cypress Hills plotted over standardized range of habitat covariates. Exponents of natural-log transformed step length are presented for ease of interpretation. Response curves are plotted only for covariates significant at the population-level (see Table 3.3)

Table 3.1: Ranging statistics for sub-adult cougars in the Cypress Hills monitored between 2010 and 2012. Straight-line distance and cumulative distance were calculated from the center point of the last temporary home range (THR) to the center point of the cougar's natal range. If multiple THRs were used by individual cougars they are denoted by cougar ID and then chronologically by letter code A or B.

Cougar	Dispersal status	Straight line distance (km)	Cumulative distance (km)	Temporary home range	Area (km^2)	Overlap w/ adult range
F1	Unk	N/A	N/A	F1_THR_A	47.44	90.04%
				F1_THR_B	71.37	78.58%
F4	Dispersed	24.53	209.62	F4_THR	95.89	66.02%
F5	Philopatric	2.88	54.57	F5_THR	75.62	84.56%
Female Average		**13.71**	**132.10**		**72.58**	**79.80%**
M3	Dispersed	40.28	200.85	M3_THR_A	229.77	52.11%
				M3_THR_B	246.93	20.00%
M7	Dispersed	108.68	271.69	M7_THR_A	21.82	0.00%
				M7_THR_B	304.33	11.50%
M9	Dispersed	25.56	235.26	M9_THR_A	79.26	17.21%
				M9_THR_B	225.88	11.66%
M10	Dispersed	486.66	749.28	M10_THR	98.79	0.00%
Male Average		**165.30**	**364.27**		**172.40**	**16.07%**

Table 3.2: Standardized population-level coefficients (β), 90% confidence intervals (C.I.) and significance (*) for sub-adult cougars in the Cypress Hills. Population coefficients were calculated by averaging individual-level betas obtained using conditional logistic regression models. Coefficients were considered significant if 90% confidence intervals did not overlap 0. Land cover was a categorical variable and used *tree* as a reference category.

	TRANSIENCE				LOCALIZING			
		90% C.I.				90% C.I.		
Covariate	**β**	**upper**	**lower**		**β**	**upper**	**lower**	
elevation	-0.821	-0.3343	-1.3082	*	-0.406	-0.067	-0.746	*
elevation^2	0.382	0.7723	-0.0093		0.278	0.935	-0.378	
TRI	0.802	1.1315	0.4717	*	0.700	1.295	0.105	*
TRI^2	-0.155	-0.0624	-0.2471	*	-0.107	-0.076	-0.137	*
hydro	-0.227	-0.1202	-0.3329	*	-0.251	-0.120	-0.381	*
hydro^2	0.109	0.2752	-0.0571		0.089	0.218	-0.040	
water	N/A	N/A	N/A		-0.064	0.236	-0.364	
water^2	N/A	N/A	N/A		-0.123	-0.104	-0.142	*
paved_rd	-0.080	0.2996	-0.4588		-0.028	0.249	-0.305	
paved_rd^2	0.073	0.1920	-0.0468		-0.205	-0.145	-0.265	*
unpavd_rd	0.201	0.5595	-0.1580		0.184	0.339	0.030	*
unpavd_rd^2	0.085	0.1808	-0.0105		-0.056	-0.041	-0.071	*
cover								
shrub	-1.080	-0.4920	-1.6688	*	-0.692	0.053	-1.437	
wetland	-0.312	0.2852	-0.9087		-0.938	-0.137	-1.738	*
grassland	-1.631	-0.9240	-2.3388	*	-1.646	-1.537	-1.755	*
agriculture	-1.831	-0.9607	-2.7005	*	-2.474	-2.342	-2.607	*
pasture	-1.096	-0.6954	-1.4965	*	-1.669	-1.322	-2.016	*

Table 3.3: Step-length model results for sub-adult cougars in the Cypress Hills estimated using linear regression. Standardized population-level coefficients (β), 90% confidence intervals (C.I.) and significance (*) are reported. Step length was natural log transformed for statistical analysis. *Day_period* used *crepuscular* as a reference category. *Ranging* used *transience* as a reference category. *Tree cover* was excluded from the model to act as a reference category for *proportional cover*.

		90% C.I.		
Covariate	**β**	**Upper**	**Lower**	**Significant**
constant	5.958	6.994	4.923	*
elevation	0.656	1.605	-0.293	
elevation^2	0.092	0.546	-0.361	
TRI	-0.215	-0.104	-0.327	*
TRI^2	-0.052	0.006	-0.111	
unpavd_rd	0.236	0.308	0.164	*
unpavd_rd^2	-0.217	-0.065	-0.369	*
pavd_rd	-0.647	0.292	-1.586	
pavd_rd	-0.229	0.221	-0.678	
hydro	0.260	0.423	0.098	*
hydro^2	-0.254	-0.077	-0.431	*
water	-0.017	0.141	-0.176	
water^2	-0.039	0.046	-0.123	
day_period				
day	-1.790	-1.362	-2.218	*
night	0.938	1.589	0.287	*
Proportional cover				
shrub	0.182	0.540	-0.177	
wetland	0.073	0.276	-0.130	
grassland	0.702	0.948	0.457	*
agriculture	0.387	0.604	0.171	*
pasture	0.481	0.828	0.133	*
ranging				
localizing	-0.739	0.696	-2.173	
day × shrub	-0.193	0.186	-0.573	
night × shrub	-0.050	0.186	-0.287	
day × wet	-0.050	0.078	-0.178	
night × wet	0.047	0.108	-0.014	
day × grassland	-0.460	-0.249	-0.670	*
night × grassland	0.252	0.468	0.035	*
day × agriculture	-0.040	0.002	-0.082	
night × agriculture	0.144	0.297	-0.009	
day × pasture	-0.154	0.136	-0.444	
night × pasture	0.197	0.343	0.052	*
day × localizing	0.294	0.910	-0.322	
night × localizing	-1.056	-0.179	-1.932	*

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CHAPTER 4

GENERAL CONLUSIONS AND MANAGEMENT RECOMMENDATIONS

Cougar (*Puma concolor*) range expansion is creating complex new challenges for wildlife managers, including balancing the ecological and social implications of a returning large carnivore. Most often, wildlife populations are managed at the state or provincial level which means when cougars cross into new political jurisdictions there is often no plan to address these challenges. In Canada, cougar sightings have increased throughout the Prairie Provinces with an established breeding population confirmed in Saskatchewan and the presence of wild cougars confirmed in Ontario (Rosatte 2011) and Manitoba (Watkins 2005). However no cougar management plans exist for any province east of Alberta (Anderson et al. 2010). In the U.S., a similar trend of cougar presence preceding the development of state management strategies is also apparent.

Understanding how cougar expansion is progressing and the associated implications for human-cougar interactions are critical components for proactive management. The goal of this thesis was to address these aspects of cougar conservation biology. By focusing on an isolated and recently re-established cougar population my results provide information for wildlife stakeholders (e.g., wildlife and natural-area managers, special-interest groups, landowners, general public) not only in the Cypress Hills but in the broader scope of cougar range expansion in North America.

In Chapter 2, I examined seasonal space-use of cougars in response to varying levels of human activity on roads and trails. My results support recent finding from other research that indicates cougars can adapt to varying levels of anthropogenic disturbances (Kertson et al. 2011, Knopff 2011) and that it is human activity rather than human infrastructure that negatively influences cougars (Arundel et al. 2007). As a whole, cougars tended to avoid roads and trails during peak summer months when human activity was greatest but did not avoid these areas, and sometimes even selected them, during off-seasons when human activity was lower. This spatial shift is likely influenced, if not driven, by a high density of prey that occurs in the core areas of Cypress Hills Interprovincial Park (CHIP) because of people providing feed for deer and birds through the winter. Numerous cases of cougars bedding and caching prey under decks and cottages have been documented in both core areas of CHIP during the winter months, which represents a real public safety concern. I recommend strict enforcement of bylaws prohibiting feeding deer and birds. In the absence of enforceable legislation, public education campaigns to promote the enclosure of decks and raised cottages that provide security for cougars also should be employed. To CHIP's credit, park administrators and Compliance Officers have begun taking these precautions. Hazing of both cougars and deer that frequent settled areas also could be considered although evidence supporting the effectiveness of aversive conditioning on cougars is limited (Sweanor and Logan 2010).

Cougars used the trails during all seasons and more cougars were documented at cameras stations in the summer and fall, than in the winter and spring. Therefore, even though cougars might avoid trails at the patch scale when human activity is high, this avoidance certainly is not absolute. Further, when in proximity of a trail, cougars may actually prefer using them as travel corridors in areas where the understory is dense (Dickson et al. 2005). Aside from seasonal shifts in habitat use, the actual level of within-season human activity measured along the trails appeared to have little effect on cougar habitat selection or whether a cougar was detected at a camera station.

In sum, the potential for human cougar interactions is present throughout the year, although there are periods such as low human-use seasons and evenings when the potential is likely highest. The high amount of variation observed among the individual-based models makes these human-cougar interactions difficult to predict. Managers should establish a formal process for the public to report their sightings so that trends and hotspots can be identified and tracked. Public education explaining basic cougar ecology, sign identification, and safety precautions likely will be the best tool for mitigating negative human-cougar interactions. Managers should use their authority to close trails when cougar activity is concentrated in an area. This will reduce the potential for conflict and reinforce with the public that cougars are a part of landscape that must be accommodated. If conflicts increase, management strategies targeted for individual cougars may be more effective than population-level controls.

Long-distance dispersal of sub-adult cougars throughout the Midwest is becoming well-documented (Thompson and Jenks 2005, 2010; Larue et al. 2012; Morrison 2013). Advances in satellite tracking technology offer tools to study fine-scale habitat use and movement of cougars as they disperse across the landscape. In Chapter 3, I used satellite-GPS collars to track the dispersal and home-ranging behaviours of sub-adult cougars in the Cypress Hills. Notably, young males used less-suitable habitats on the fringes of this isolated population. In the Cypress Hills this spatial demographic structure means that habitats outside the protected areas likely have higher relative densities of sub-adult cougars. In other studies, cougar populations with young age structures have been linked to increased rates of conflict with people (Lambert et al. 2006). The observed spatial distribution of sub-adult THRs further increases the potential for conflict because the landscape surrounding CHIP provides less forested cover and is dominated by private ranch lands with more residence and livestock.

Although the potential for conflict is predicted to be greater where sub-adult cougars and humans heavily overlap, negative conflict between people and cougars (i.e., aggressive encounters and livestock depredation) in the Cypress Hills appears to be rare. Cumulative research efforts in the hills have failed to document any evidence of livestock depredation despite visiting over 650 kill sites and analysing 211 scat samples (Bacon et al. 2011, Morrison unpublished data). These data should help ease landowner’s concerns regarding the threats of cougars to their livelihoods. Regardless, landowners in both Alberta and Saskatchewan have the right to shoot cougars in defence of themselves or their property and cougars are occasionally killed under this legislation. This was illustrated by cougar M3's life history who shifted his temporary home range outside the park, apparently to avoid conflict with resident cougars, and was later presumably killed by humans because only his collar, which had been unfastened, was recovered at his last known location. In Alberta, the recent introduction of a "boot" season (i.e., use of hounds and electronic calls is prohibited) in the Wildlife Management Units that surround CHIP further increases the likelihood of human-caused mortalities for cougar venturing outside the protected area. However, this source of mortality is likely not significant – only one cougar has been harvested during the two years since the hunt was introduced (N.Webb, Alberta Sustainable Resource Development, personal communication, 2013).

My research supports initial findings by Bacon (2010) that documented high home range overlap by adult cougars in primary habitat patches. Female cougars tend to be more tolerant of conspecifics, especially kin. This accommodates the high rate of philopatry observed with sub-adult females (Sweanor et al. 2000). In the initial stages of cougar re-colonization, smaller isolated patches may be able to support higher densities of cougars because prey are relatively naive, prey abundance might be high and there might be a high degree of relatedness (i.e., conspecific tolerance) among colonizing cougars. Additional research examining the genetic relatedness of cougars during cougar re-colonization would be required to test this hypothesis. Female dispersal is theorized to be partially density dependent (Logan and Sweanor 2001). As competition for resources increase I suspect that more female dispersers will appear which is required for cougars to re-colonize other suitable habitat further east.

Immigration and emigration will be necessary for the long-term persistence of isolated populations of cougars separated by wide expanses of grassland-dominated habitats. In this regard, this thesis quantifies cougar habitat selection and movement patterns of sub-adult cougars in this Midwestern landscape. This has applications for evaluating potential corridors that could facilitate cougar dispersal such as riparian and forested habitats and rugged terrain (LaRue and Nielsen 2008). However, cougars will not necessarily restrict movements to these preferred habitat types. When moving through open flat terrain cougars shifted to longer and more nocturnal movements. This strategy enables cougars to limit their residency and exposure when moving through large expanses of relatively unsuitable habitat which may inherently reduce the potential for interacting with people. This ability to remain undetected in these atypical habitats likely has contributed to the success of cougar range expansion thus far.

On the other hand, when cougars are detected in these novel landscapes this can raise concerns with a relatively naive public. For instance a young male cougar near the Cypress Hills was deemed a potential threat and destroyed by wildlife officials when it was discovered in a culvert close to a rural residence. As young cougars disperse eastward these types of encounters are likely to increase. On several different occasions during this study dispersing sub-adult cougars were observed taking day-time refuge in cover associated with human infrastructure including abandoned-car yards, rural residence and other man-made structures (Fig. 4.1). In these cases, cougars occupied these sites only during day-light hours and continued dispersal under the cover of darkness. These observations support my step-length model results and can be used to inform wildlife managers and the public with alternative management strategies. For example, referring back to the young cougar in the culvert, in all likelihood, this animal was seeking shelter for the day and would have been far removed from the residence the following night. Providing the landowner with information on cougar dispersal ecology, good husbandry practices for pets and livestock, and personal safety precautions would have likely limited the risk of a negative interaction and might have forgone the need to kill the animal.

Considering chapter 2 and 3 together, my thesis sheds light on how other areas might be re-colonized by cougars. Human activity may influence cougar spatial ecology but at tolerable levels it likely will not be a limiting factor in cougar re-colonization. High densities of human development and high human activity, such as residential areas and highways, still should be considered unsuitable habitats and potential barriers to movement (Kertson et al. 2011, Maehr et al. 2002). I recommend proactive monitoring of other natural areas that could potentially be re-colonized, or may already support transient cougars, to track the distribution and re-establishment of cougar populations east of their contemporary range.

Cougar use of roads and trails is prevalent (Morrison 2013, Kertson et al. 2011, Dickson et al. 2005). As such, camera traps deployed on roads and trails are an efficient, cost-effective method for monitoring the presence of cougars in other areas. For example, a camera survey not targeted for cougars confirmed the presence of at least one other cougar in Moose Mountain Provincial Park prior to the arrival of M10 that dispersed from the Cypress Hills (J. Karst, Saskatchewan Fish and Wildlife, 2012, personal communication). Moreover, cameras can document the presence of breeding which is a prerequisite for a population to become established. Cameras set up by Conservation Officers were one of the first methods to provide evidence of breeding in the Cypress Hills population. Further, my camera survey documented several additional instances of family groups and at least 2 different mating associations (i.e., a mature male and female travelling together) at three different camera sites. Despite the benefits of camera monitoring, camera theft was a problem in my study area. Although cameras were camouflaged, code-locked, chain-locked to trees, fitted with a label explaining the purpose of the camera, and not deployed in year-round high-traffic areas, a total of 6 cameras (representing 16% of all cameras) were stolen during the course of the 12 month sampling period. Future studies employing cameras should recognize this risk.

The cougar’s ability to disperse great distances, their role as an apex predator, and their relative tolerance of human activity make the cougar a candidate focal species for large-scale conservation planning. Jurisdictions experiencing an increase in cougar sightings will benefit by developing proactive management strategies and clear protocols to promote the conservation of this species. Pre-emptive monitoring programs and public education initiatives will play a critical role in disseminating accurate information, increasing public tolerance and reducing the potential for human-cougar interactions. At the local level my thesis provides information for cross-border adaptive management strategies and will serve to inform and educate stakeholders who have an interest in the management of this species in the Cypress Hills. In a broader context, an improved understanding of the cougar’s ability to re-colonize isolated patches of habitat and coexist with humans offers hope for cougar conservation in a rapidly changing landscape.

A)

B)

Figure 4.1: Examples of cougar day-time GPS locations associated with human infrastructure during dispersal. In both cases, cougars continued dispersing under the cover of darkness and never returned. A) Cougar M7 remained at this rural residence from 0600 h to 2100 h and was located 2.5 km away at his 2400 h fix. B) Cougar M10 recorded fixes at 1200 h and 2100 h at an abandoned-car yard and was located 6.1 km away at 2400 h. Prior to forming this cluster, M10's last successful fix was 0300 h. His 0600, 0900, 1500 and 1800 h fixes were unsuccessful presumably because he was under a vehicle.

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