Space use dynamics and habitat selection of cougars in west-central Alberta, Canada

by

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Abstract

The choices animals make such as what habitat to use or where to live are influenced by individual behavior and life history traits. Gaining insight on space use patterns and habitat selection of a species can help wildlife managers in understanding social dynamics, population size and density, as well as identifying high-quality habitats that can be managed accordingly. For large solitary carnivores, such as cougars (*Puma concolor*), prey, mates, and safe habitat to raise offspring are resources that influence space use and habitat selection. In Alberta, human-cougar conflict has increased since the mid 1990s and management actions need to be taken to reduce conflict with people while maintaining a viable population. Information on cougar space-use patterns and habitat selection should be considered before management actions are prescribed. Thus, my main objectives were to: 1) develop methods that could be used to determine the different space-use patterns used by cougars, and 2) develop resource selection functions (RSF) for cougars of different sex and reproductive statuses during snow and snow-free periods. For my first objective, I used a combination of net-squared displacement, path-segmentation analysis, and multi-response permutation procedure to examine variation in space use patterns for 27 female and 16 male cougars in west-central, Alberta, Canada from 2016-2018. With the three analyses, a decision tree was constructed and I found that cougar home ranges were dynamic, with space use changing over time for many individuals. We fit four space use patterns: dispersers (12% of females and 44% of males), residents (58% of females and 31% of males), seasonal home range shifters (12% of females and 6% of males), and individuals that shifted to a new area during the study period (19% for females and 19% of males). For my second objective, I used a two-step resource selection function to identify seasonal habitat characteristics used by 55 adult cougars. We analysed habitat use in three groups of cougars:

adult males, single females, and females with kittens. All groups selected for similar habitat types including edge habitats, close proximity to water, sloped terrain, forested habitats, and avoided roads. During the summer, close proximity to water and wetland land cover were among the most selected habitat features for all groups. Forest and edge habitats also were important for single females and males. During the winter, forested habitat was one of the most important covariates for all groups along with close proximity to water, edge habitat and slope for single females and males. Slope and open agricultural land were among the most important for females with kittens. My first chapter provides insights on animal home ranges with methods to categorize different space use strategies which may be applied to other species or systems. Furthermore, information on space use patterns may assist in understanding the social structure of a population and whether cougar harvest levels need to be altered. The results of my RSF can provide information on where higher-quality habitats occur and could be used by wildlife managers to identify source and sink populations and to implement harvest strategies to maintain a viable population while minimizing human-cougar conflict.

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Chapter 1

1 Introduction

The introduction of radio-telemetry data in the mid 1900s (Craighead and Craighead 1972) and the further technological advancements of GPS collars in the 1990s (Rodgers 1996), has enabled researchers to acquire detailed movement data that can be used to answer questions about animal ecology such as home range size, territoriality, and space use patterns (Siniff and Jessen 1969). A home range or territory is maintained and defended in an area where sufficient resources such as food, mates, and shelter are available (Burt 1943, Schoener 1968, Brown and Orians 1970, Powell 2000). Attributes of a home range, such as size or shape, have adaptive significance to the species in question (Schoener 1981, Swihart et al. 1988). Radio-telemetry has allowed researchers to examine the habitat attributes that animals select within their home range. Home range size is a suitable predictor of a species' feeding strategy and is associated with that animal's locomotion, metabolic needs, and access to resources (Schoener 1971, Simon 1975). Animals with a larger body size are generally less constrained by their physical environment and capable of travelling greater distances in search of food, therefore influencing the size of their home range (McNab 1963, Tamburello et al. 2015). However, body size has an additional effect on home range size independent of locomotion. As a consequence of allometry, larger bodied animals have a higher metabolic demand for basic physiological maintenance and must consume more calories to survive (McNab 1963, Tucker et al. 2014). For most vertebrates, home range size and habitat productivity are negatively related, with higher habitat productivity decreasing home range size and vice versa (Harestad and Bunnell 1979, Lindstedt et al. 1986). Most animal home range and territory studies assume home ranges are static and focus on size and factors that might affect it. However, animal space use is dynamic and this has largely been ignored in the past and only recently identified as an important aspect of population dynamics and animal ecology (Mosnier et al. 2003, Wang and Grimm 2007, Šklíba et al. 2009). Studies on animal space use dynamics often focus on migratory species where large differences in spatial distribution make analyses robust and easily replicated (Boone et al. 2006, Mandel et al. 2008, Bailey et al. 2009, Singh et al. 2012). However, individuals within a population may have variable space use strategies depending on regional variation in factors such as food availability (Gittleman and Harvey 1982, Jones 1990, Wiktander et al. 2001), mate availability (Macdonald 1983, Sandell 1989, Goodrich et al. 2010), habitat quality (Santangeli et al. 2012, Knüsel et al. 2019), and population density (Hoset et al. 2007, Efford et al. 2016). Gaining knowledge on if and how space use is dynamic within a population can help to understand the social stability and structure of a population.

Throughout their life, animals make behavioral choices of what resources to use versus what is available on the landscape. The extent to which resources are selected or avoided typically reflects the quality of habitat and thus influences an individual's reproductive success and survival (Southwood 1977). If the distribution of available resources and locations used by an individual are known, a resource selection function (RSF) can be used to develop models to quantify the probability of use of a resource unit and map the distribution of high or low quality habitat (Boyce et al. 2002).

Fitness consequences of a species or individual are proportional to the scale at which behavioral decisions are made (Mayor et al. 2009). For instance, there will be less of a fitness consequence when choosing to hunt in a small patch of forest where there are few prey compared to choosing a home range where there are few prey. Depending on the ecological question, RSFs are developed at varying scales. Johnson (1980) described four scales of selection at which animals make choices. First order of selection occurs at the species geographic range; second order is where the individual selects a home range; third order is what an individual selects within a home range; and fourth order relates to fine-scale use of habitat such as the selection of food types compared to what is available within a foraging site.

Most RSF studies occur at the second or third order of selection and are regarded as most important when trying to realize population level habitat selection. Although second order selection describes an individual's selection of a home range, the choices made at this scale are guided by the immediate resources they encounter and whether they are perceived as high or low quality (Kokko and Sutherland 2001, Kristan 2003). Therefore, third order of selection can also be used to analyze population level habitat selection if multiple individuals are making the same decisions within their home range (Garabedian et al. 2014, Marchand et al. 2015).

Cougars (*Puma concolor*) are adaptable and thrive in a variety of ecosystems across North and South America, making them one the widest ranging mammals in the world (Jenks 2011). Historically, cougars spanned from northern Alberta and British Columbia, Canada, to as far south as Chile (Yáñez et al. 1986). Because of human encroachment, habitat loss, and human intolerance cougars were extirpated from two-thirds of their range by the early 1900s (Anderson et al. 2010). However, with the increase in science-based management, human tolerance, prey abundance, and habitat changes, cougars have begun to recolonize their native range in western North America (Riley and Malecki 2001, Jenks 2011).

In Alberta, substantial ungulate population decline as a result of early European settlement, severe winters, and unregulated hunting, were likely responsible for the decline in cougar numbers in the early 1900s (Knopff et al. 2014). By the mid-1900s ungulate populations had recovered and cougar harvest restrictions were enacted, which in combination, were likely responsible for reversing the trend of cougar population decline in Alberta. Since the early 1990s cougar populations in Alberta have expanded (Knopff et al. 2014). The growing population has led to increasing human-cougar conflict, ultimately resulting in higher rates of human-caused cougar mortality (Government of Alberta, unpublished data). A combination of landowner harvest, problem cougar removal, incidental trapping, and licensed harvest are responsible for the majority of human-caused cougar mortality, with less than 50% of mortality coming from licensed resident hunters in some years (Alberta Environment and Parks, unpublished data). To maintain a viable cougar population and decrease human-cougar conflict, proper management actions need to be followed.

Adult cougars live primarily solitary lives and social interactions generally occur during mating or territorial defense (Sandell 1989, Sunquist and Sunquist 2017). Adult males are territorial against competing males and may breed with numerous females that overlap his territory (Logan and Sweanor 2001). Similar to other felids, female cougars are polyestrous and generally mate with the resident male that occupies their home range (Beier 1995, Logan and Sweanor 2001), but may also adopt a promiscuous breeding strategy if the population is unstable to reduce the risk of infanticide and aggression from males (Logan and Sweanor 2009). Unlike males, females are not territorial and instead expend their energy hunting and raising offspring while avoiding interactions with other cougars (Logan and Sweanor 2009).

Primiparity for female cougars can vary, and their first litter can occur from 16 to 30 months of age (Ross and Jalkotzy 1992, Lambert et al. 2006, Logan and Sweanor 2010). Although they can breed at any time of year, cougars tend to have a birth pulse from May to October (Laundré and Hernández 2007). The timing of the birth pulse likely corresponds to a peak in vulnerable ungulate prey and allows the female to provide her energetically demanding offspring with sufficient nutrients (Logan and Sweanor 2001, Laundre and Hernandez 2007). Every 17 to 24 months female cougars may produce a litter of 1 – 6 altricial offspring (Young and Goldman 1946), however mean litter size is 2 – 3 kittens (Ross and Jalkotzy 1992; Logan and Sweanor 2010). Kittens are born in a natal den where they are protected from predators and infanticide (Logan and Sweanor 2001). During the first 2 to 3 months of life kittens are immobile, stay at the nursery site, are most vulnerable, and are entirely dependent on their mother (Seidensticker et al. 1973). At 6 months, kittens are still reliant on their mother and are unable to survive on their own with the primary cause of death being starvation (CMGWG 2005). Kittens will remain with their mother for 10 – 33 months (Logan and Sweanor 2009; Jenks 2011) and will disperse after the female abandons them near the edge of her home range (Seidensticker et al. 1973; Beier 1995).

To support their highly dependent offspring, female cougars generally establish a home range that will provide her with sufficient resources, such as prey and protection from predators and conspecifics (Logan and Sweanor 2001). Female home range size is smaller than males and ranges from 55 - 300 km^2. Males have no direct contribution to raising offspring and are able to traverse greater distances, resulting in territories that are up to 700 km^2 (Logan and Sweanor 2009). Both sexes are believed to have high fidelity to a range as it may be beneficial to occupy familiar territory where they have knowledge of mate locations, quality hunting areas, and escapes routes (Logan and Sweanor 2009). However, fidelity may break down over time, and this is especially true for males (Logan and Sweanor 2001). Male territory boundaries tend to be dynamic and are associated with competition from neighboring or subadult males.

In Chapter 2, I investigate home range dynamics as well as home range size of independent cougars in west-central Alberta, Canada. In this chapter, I present a method that can be used to distinguish different space use patterns of cougars that may be applicable to other species. In Chapter 3, I use a RSF to determine habitat variables that are selected or avoided by adult male, single female and female cougars with kittens, and whether differences in selection occur between seasons of winter and summer (snow versus snow free). The results of Chapter 3 may help wildlife managers in distinguishing where source and sink populations occur and whether management zone boundaries or harvest quotas should change. In Chapter 4, I discuss how my research may be used in cougar management and conservation and future directions for cougar research.

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Chapter 2

2 Home-range and space use characteristics of cougars at the northern edge of their range

2.1 Introduction

A home range is the area used by an individual animal, where it performs normal behaviors, such as avoiding predation, competing against conspecifics, locating mates, raising offspring, and foraging (Burt 1943, Powell 2000). The life history of a species and individual decision-making influence how animals use space to acquire resources to increase fitness (Börger et al. 2006, Mitchell and Powell 2012, Knüsel et al. 2019). Both intrinsic and extrinsic factors influence how an individual uses the landscape (Börger et al. 2006, Larroque et al. 2018). Assessing home ranges and spacing behavior of conspecifics is important for understanding autecology (Lendrum et al. 2014, Bateman et al. 2015), social dynamics (Seidensticker et al. 1973), and for estimating population size and density (Gros et al. 1996, Duncan et al. 2015).

Home range sizes can vary across a species' range (McLoughlin et al. 2000, Nilsen et al. 2005, Loveridge et al. 2009, van Beest et al. 2011) and is influenced by food availability (Gittleman and Harvey 1982, Jones 1990, Wiktander et al. 2001), habitat (Santangeli et al. 2012, Knüsel et al. 2019), and population density (Hoset et al. 2007, Efford et al. 2016). Furthermore, population density affects resource availability and is inversely related to home range size (Hoset et al. 2007, Šálek et al. 2015). Home range size is also affected by sex, with males typically having larger home ranges than predicted by their food requirements alone (Clutton-Brock and Harvey 1978, Cederlund and Sand 1994, Schmidt et al. 1997, Logan and Sweanor 2001).

Territorial behavior can also influence home range size and space use patterns of animals and is common in carnivores, such as mustelids, canids, and felids (Noble 1939, Sandell 1989, Mech 1994, Logan and Sweanor 2001, Hedmark et al. 2007). Many carnivores exhibit intrasexual territoriality where intrusion of the same sex onto a resident's territory can lead to aggressive interactions (Boydston et al. 2001, Logan and Sweanor 2001). Even so, territories are dynamic and direct conflicts with, or removal of conspecifics can result in contraction or expansion of a home range (Gese 1998, Logan and Sweanor 2001). Although variability in these factors can result in differences in home range size across a species distribution, changes at the regional level may result in dynamic space use patterns of individuals within a population (Edwards et al. 2009). Unlike social carnivores, many solitary carnivores, including most felids, have a polygynous mating strategy and rarely interact except when breeding (Sandell 1989, Logan and Sweanor 2001). Males in these species do not contribute to raising offspring and typically have home ranges that overlap multiple females to maximize mating opportunity but are territorial against intruding males (Sandell 1989, Chundawat et al. 2016). Females have smaller home ranges that can provide resources for her and her offspring as well as protection from predators or unfamiliar males that may commit infanticide (Amstrup et al. 2001, Logan and Sweanor 2001, Singh and Ericsson 2014). For both sexes, it may be beneficial for individuals to remain in familiar surroundings instead of venturing into an occupied territory where aggression from the resident individual, and potential mortality can occur (Logan and Sweanor 2001). However, high population density, insufficient food or mates, or mortality events that free occupied habitat may result in dynamic space use (Loveridge et al. 2007, Edwards et al. 2009, Zalewski 2012, Aronsson and Persson 2018).

Space use patterns may include dispersal (e.g., Bowler and Benton 2005, Almany et al. 2017), resident (e.g., Kamler and Gipson 2000, Hauser et al. 2007), migration or seasonal shifts (e.g., Festa-Bianchet 1986, Phillips et al. 1998), and shifting or drifting home ranges (e.g., Doncaster and Macdonald 1991, Edwards et al. 2009). Dispersal is the unidirectional movement away from the natal range and is predominantly displayed by young individuals in search of a new territory (e.g., Sweanor et al. 2000, Bowler and Benton 2005). Residents have high fidelity to their home range and the reuse of an area may result in spatial familiarity, enhancing the individual's ability to locate resources or refuges (Krebs 1971, Switzer 1993, 1997, Janmaat et al. 2009). Regardless of the benefits of home range fidelity, individuals may move if resources become fully exploited or there is a lack of mates, causing a shift in space use and a dynamic home range (Doncaster and Macdonald 1991, Edwards et al. 2009, Aronsson and Persson 2018). When resources are low, animals may migrate (Dingle 1972, Fryxell and Sinclair 1988), or residents may shift their space use seasonally to regions of their home range where resources are more abundant (Walton et al. 2001, Szemethy et al. 2003, Dellinger et al. 2018). Finally, a shifting home range is the result of expansion in one direction and reduction in another and may be caused by changes of social structure and stability in a population or food availability (Doncaster and Macdonald 1991, Edwards et al. 2009).

Cougars (*Puma concolor*) have the largest geographic range of any New World felid and occupy a wide range of climates and habitat, from the temperate forests of Canada and the northern United States, to the tropical ecosystems of South America (Nowak and Walker 1999, Jenks 2011). Cougars typify the characteristics of solitary, territorial carnivores with a polygynous mating strategy, male-male territorial defense, and females avoiding but tolerant to one another (Seidensticker et al. 1973, Logan and Sweanor 2001). Adult males typically have a home-range size that encompasses multiple adult female ranges (Logan and Sweanor 2001). Adult female home-ranges tend to be only large enough to include sufficient prey and safety for her and dependent offspring (Sandell 1989, Logan and Sweanor 2001). Females are induced ovulators and can breed any time of year (Beier 1995, Laundré and Hernández 2007), therefore, males are likely to express territorial behavior throughout the year to maximize their chances of breeding success (Logan and Sweanor 2010). At between 10-33 months old, subadult cougars leave their natal range with males typically dispersing and females remaining philopatric or dispersing a short distance (Sweanor et al. 2000). Numerous studies have examined cougar home range size (Ross and Jalkotzy 1992, Spreadbury et al. 1996, Sweanor et al. 2000, Maletzke et al. 2014, Elbroch et al. 2016) however, little information is available on the different space use patterns that may occur in a population and how these patterns vary by age and sex.

The main objective of this study is to examine cougar home range size and dynamics. I examine home range patterns by age and sex in west-central, Alberta, Canada, by comparing annual home range size of independent cougars. Based on carnivore ecology, I predict that cougar space use will fall into four categories: dispersers, residents, seasonal shifters, and shifters. I predict that dispersers will include subadults of both sexes. I predict residents will include both adult males and females. I predict that some adults of both sexes may exhibit a seasonal shift within their range to utilize heterogeneous prey distributions, and for females, avert dangerous males and avoid regions of high activity with overlapping conspecifics. Finally, I predict that shifters will include males and females. Because of fluctuation in territory boundaries from intrasexual competition, habitat vacancies due to removal of a neighboring male, and searching for prospective mates, shifting home ranges in males may be more common than in females. However, adult females may also shift their range when a neighboring area becomes vacant or the social structure of the population becomes unstable.

2.2 Methods

2.2.1 Study Area

Our study was conducted from 2016 to 2018 in west-central Alberta, Canada (Figure 2.1). The study area (ca. 77,327-km^2) is a mix of farmland, rural properties, and forested habitats with higher human disturbance to the east (Knopff et al. 2014). The area borders the Rocky Mountains to the west and extends east to the towns of Whitecourt and Rocky Mountain House with the landscape transitioning from mountainous terrain at the western boundary to rolling foothills and then agricultural lands to the east. The region contains upper foothills, lower foothills, subalpine, alpine and central mixed-wood ecoregions (Natural Regions and Subregions of Alberta. 2006). Coniferous forests of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) dominate the region, with tamarack (*Larix laricina*) and black spruce (*P. mariana*) more common near wetlands and in lower elevations (Government of Alberta, 2011). Deciduous trees include balsam poplar (*Populus balsamifera*) and aspen (*P. tremuloides*) scattered throughout the region but are more common in the east and north. The climate is characterized by wet springs, warm and dry summers, and cold winters with heavy snow falls (Strong 1992). Linear features (e.g., roads, pipelines, seismic activity) are common due to forestry and hydrocarbon extraction activities. Cougars are harvested in Alberta and the study area covered three cougar management areas (CMAs 11, 12, and 21). In addition to harvest, there are high rates of human caused cougar mortality through removal of problem cougars and landowner take (Government of Alberta, unpublished data).

Numerous potential prey occur in the region. Larger prey include moose (*Alces alces*), elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and feral horses (*Equus caballus*). Bighorn sheep (*Ovis canadensis*) and mountain goat (*Oreamnos* *americanus*) are less abundant and found mostly to the west. Smaller prey includes red fox (*Vulpes vulpes*), beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), snowshoe hare (*Lepus americanus*), and ground nesting birds such as ruffed grouse (*Bonasa umbellus*) and spruce grouse (*Falcipennis canadensis*). Cougar may also prey on domestic animals. Other predators include wolves (*Canis lupus*), coyote (*C. latrans*), black bears (*Ursus americanus*), grizzly bears (*U. arctos*), wolverine (*Gulo gulo*), and lynx (*Lynx canadensis*).

2.2.2 Cougar Capture and Monitoring

Cougars were caught from late autumn to early spring using snow tracking and trained hounds to tree study animals. Cougars were immobilized with a Dan-inject CO2 rifle and dart using the drug combination Telazol® (1.7-2.6 mg/kg) and medetomidine (0.05-0.075 mg/kg), and then recovered after reversal of medetomidine with atipamezole (0.4 mg/kg) (Government of Alberta). Immobilized cougars were collared with Vectronics Vertex Lite VHF/GPS radio collars (Vectronic Aerospace, GmBh, Berlin, Germany), ear tagged, weighed, and aged using gum-line recession, tooth color and wear, and pelage spotting and barring (Laundré et al. 2000, Heffelfinger 2010). GPS locations were recorded at 4-hour intervals for females with kittens and 7-hour intervals for all other individuals, with locations received via satellite. Collars had a cotton rot-away and fell off the cougar 2-3 years post capture or were removed on recapture or harvest. All procedures followed ASM guidelines (Sikes et al. 2016) and were in accordance with the Alberta Wildlife Animal Care Committee Class Protocol #12 (Research Permit 5986) and were consistent with the Canadian Council on Animal Care.

2.2.3 Data Standardization

I limited my analyses to independent cougars and excluded subadults travelling with their family until they were independent. Because immobilization and capture procedures may affect animal movement patterns (Thiemann et al. 2013), I removed the first 5 days of location data to reduce the effects of handling on movement in analyses. Because of differences in collar fix rate, I resampled GPS data to 1 location/day as suggested by Bunnefeld et al. (2011). To standardize home range comparisons across individuals, I first identified individuals with an asymptotic annual home range size using kernel density area observation plots generated in the rhr package in R (Signer and Balkenhol 2014). I plotted the first 30 locations and increased the sample by 30 until all GPS locations were used for one year. I defined individuals as having an asymptotic annual home range if the area remained within the 95% confidence interval for five sets of 30 consecutive locations (150 locations) (Laver and Kelly 2008). To further standardize annual home range estimates, I determined the number of days of locations required to achieve 90% of the annual home range estimate to asymptote. This standardized period was obtained by calculating the annual home range size for every 30 days decreasing from 365 days until a 10% change was reached and this period was used for analyses. My approach allowed us to generate comparable annual home range estimates and space use patterns while retaining more individuals in my analyses. Space use pattern analysis was also done using 365 days to detect if changes in space use patterns occurred with added data.

2.2.4 Annual Home Range Estimation

I estimated cougar annual home ranges for the year post-capture using 95% minimum convex polygon (MCP) and Brownian bridge home range (BBHR). The 95% MCP allows comparison to other studies (Harris et al. 1990). The BBHR method accounts for the relocation probability between GPS locations that are within specific time parameters as well as potential bias from spatial autocorrelation (Horne et al. 2007, Olsen et al. 2018). I defined the BBHR home range as the 95% isopleth of the utilization distribution, which removed outliers. I estimated sig1, the Brownian motion variance from a maximum likelihood estimate to predict the unknown location of an animal, and sig2, the mean location error of GPS locations (set at 15 m) for BBHR (Horne et al. 2007). All home ranges were estimated using the package adehabitatHR in R (Calenge 2011).

2.2.5 Space use patterns

I used three analyses and a decision tree (Figure 2.2) to define space use patterns for the cougars used in the home range estimation. First, I used the package migrateR in R to fit nonlinear functions to the annual net squared displacement (NSD) of individuals (Spitz et al. 2017). NSD measures the squared distance from the start location to each subsequent location. MigrateR uses five *a priori* models to classify animal movement behavior and identifies the best supported model using Akaike information criteria (AIC) (Akaike 1974, Burnham and Anderson 2002). Following Spitz et al. (2017), the five models are migration, mixed-migration, dispersal, resident, and nomad. Although cougars are non-migratory, I hypothesized that the migration model could detect seasonal shifts in home range use (i.e., seasonal shifter). I use the terms seasonal shifter, disperser, resident, and shifter to define space use patterns and omitted the mixed migration model.

Following Spitz et al. (2017), a disperser was represented with a single sigmoid curve by:

$$NSD = \frac{\delta}{1 + exp\left(\frac{\theta - t}{\varphi}\right)}$$

where δ is the distance between ranges, θ represents the midpoint of dispersal, *t* is time from start, and φ is the time required to complete ½ to ¾ of the of the movement between natal range and home range.

A resident was represented by:

$$NSD = \gamma * [1 - exp(\kappa * t)]$$

where γ is the mean NSD of all locations in a range and κ is the log of the rate constant which is used to quantify the period of increase needed for NSD to reach γ.

A shifter was represented by:

$$NSD = \beta * t$$

which is based on diffusion-based movement where β is a constant and annual NSD is expected to increase linearly over time.

Individuals may utilize different areas of their home range during different times of year, resulting in departure and return events and a double sigmoid line in an individual's annual NSD for the migration model. Therefore, seasonal shifter was represented by:

$$NSD = \frac{\delta}{1 + exp\left(\frac{\theta - t}{\varphi}\right)} + \frac{\delta}{1 + exp\left(\frac{\theta + 2 * \varphi + 2 * \varphi_2 + \rho - t}{\varphi_2}\right)}$$

where ρ is the time the individual spent in the region it shifted to.

Because individuals have variable movements and range sizes, the parameters δ, θ, φ, and γ were adjusted for each cougar for model convergence. Because some individuals went on excursions, I set ρ to a minimum of 30 days to avoid categorizing excursion events as seasonal shifts. Individuals were grouped into one of the four movement behavior classifications using AIC. If an individual had a model fit as dispersal for the annual NSD analysis, the individual was categorized as a disperser (Figure 2.2). Following the decision tree, individuals that had a model fit of resident, seasonal shifter, or shifter were further analyzed.

Second, annual NSD had the number and location of change points estimated following Lavielle (1999, 2005). Lavielle's method divides an animal's movement path into segments based on homogenous segments of NSD mean and variance. The resulting breaks in the annual

NSD allowed us to identify segments of a path and potentially indicate a change in range use. If cougars had a model fit of resident in the first step of the analysis, but did not have any segment breaks, they were categorized as residents (Figure 2.2). Individuals that had segment breaks were further analyzed using a multiple response permutation procedure (MRPP).

The third method, a MRPP, was used to compare the X and Y coordinates between the movement trajectory segments for each individual with breaks in their annual NSD (Mielke Jr et al. 1976, Edwards et al. 2009). MRPP assesses homogeneity between groups and uses a chance-corrected, within-group, agreement statistic (A) to determine if a difference between groups are greater than expected by chance. If locations between groups of X and Y coordinates are identical, $A = 0$; whereas, when groups are spatially separated, $A > 0$. In ecology, an A statistic of < 0.1 is common and 0.3 is considered high (McCune et al. 2002). Statistical significance may occur when "A" (effect size) is small, however the ecological significance must be considered (McCune et al. 2002). Therefore, I considered groups of X and Y locations with $A \geq 0.1$ biologically significant. Cougars that had segment breaks in their NSD but had $A < 0.1$ were categorized as residents (Figure 2.2). Individuals with $A \geq 0.1$ indicated significant shifts and cougars that shifted their range but returned, were categorized as seasonal shifters, while cougars that shifted their range but did not reuse a portion of their previous range (expanding their home range on one edge and contracting on another) were considered shifters (Figure 2.2). Analysis was conducted in R using the *vegan* package (Oksanen et al. 2010). Statistical significance level was 0.05. Means are presented with ± 1 SE.

2.3 Results

I collared 72 subadult (n = 25) and adult (n = 47) cougars, 48 (67%) females and 24 (33%) males. The mean age was 3.5 ± 0.2 years old (range = 1 - 9 years).

2.3.1 Data Standardization

A kernel home range asymptote was reached for 11 cougars within 365 days (mean = 248 ± 23 days, range = 154 – 364 days), and I based my annual home range standardization from these individuals. A 10% change in home range area from the 365-day estimate occurred at 270 days, and I used this period to standardize annual home range estimates.

2.3.2 Annual Home Range Size

Of the 72 collared cougar, 43 (27 females and 16 males) had ≥ 270 days of location data (mean = 837 ± 43 locations, range = 401 – 1408 locations), and MCP and BBHR home ranges were estimated for these individuals at the 270-day period using 1 location/day. Thirty-seven other cougars either died (n = 15 non-capture related human caused death, n = 2 starvation, n = 2 unknown, and n = 1 killed by wolves), had a failed collar (n = 5), were not independent of their family group (n = 3), or had inadequate data (n = 9) and were excluded from the analysis. There was no significant difference in annual home range size between subadult males and subadult females (Mann-Whitney *U* test, MCP, W = 3, p = 0.08, r = 0.41; BBHR, W=6, p =0.13, r = 0.33) (Table 2.1). Both MCP and BBHR annual home range estimates were significantly larger for adult males than adult females (Mann-Whitney *U* test: MCP, W = 14, p < 0.01, r = 0.59; BBHR, W=9, p < 0.01, r = 0.73) (Table 2.1).

2.3.3 Space use strategy

I found four space-use patterns in cougars based on the three space-use analyses following the decision tree (Figure 2.3). The space-use patterns defined were disperser, resident, seasonal shifter, and shifter. One adult female had irregular movement and could not be grouped into any of the strategies. As predicted, all 10 dispersers were subadults (mean age at dispersal = 1.7 ± 0.1 years, range = 1.2 to 3 years). Two females dispersed a short distance, while another one settled in an area overlapping her natal range (dispersal distance 14 ± 4 km, range = 8 to 21 km). All males dispersed away from their natal range (dispersal distance 101 ± 13 km, range = 37 to 135 km). Most adult female (58%) and male (63%) cougars were residents, utilizing their annual home range throughout the year. One male of 11 subadults had a resident space use strategy. Three adult females (12%) and 1 adult male (13%) were defined as seasonal shifters, identified by their non-uniform annual range use with return to a region after leaving it. Five adult females (22%) and 3 males (38%) shifted their home ranges. The pooled 95% MCP and BBHR annual home range size for each space use pattern was highly variable (Table 2.2) and individual space use patterns were diverse (Table 2.3). Nineteen cougars had 365 days of data and space-use pattern comparison at 270 and 365 days revealed that 2 individuals had a change in pattern from resident to seasonal shifter with the added data.

2.4 Discussion

My analyses revealed that cougar home range size and dynamics varied by age, sex, and individuals. Studies of animal space use often ignore the dynamic aspects of home ranges and focus on defining a single metric for a population or sex (Boone et al. 2006, Mandel et al. 2008, Bailey et al. 2009, Singh et al. 2012). Few studies examine variation in space use that do not fit the conventional categorizations of residency or migration. My analysis identified four space use patterns used by cougars. The R package migrateR was developed to study space use strategies of migratory species. Alone, it was able to successfully identify the space use pattern of 90% of cougars and with the addition of track segmentation and MRPP analyses I was able to create a decision tree and group all individuals into a space use pattern. My analyses indicated that because of the dynamic annual home ranges, a minimum of 270 days of data was sufficient to identify space use patterns given that only 11% of cougars with additional data to 365 days changed their pattern of space use. I found that cougars were flexible in the way they responded to various environmental or social factors, and their response to these factors is to change their space-use pattern.

2.4.1 Annual Home Range Size

Across North America, annual home range size of adult cougars is variable and depends on several factors including prey density, habitat quality, and social structure (Seidensticker et al. 1973, Logan and Sweanor 2001, Grigione et al. 2002). The MCP and BBHR annual home range size of 181 km^2 and 217 km^2 for adult females and 498 km^2 and 547 km^2 for adult male cougars, respectively, in my study were comparable to other cougar populations in North America (Ross and Jalkotzy 1992, Spreadbury et al. 1996, Sweanor et al. 2000, Maletzke et al. 2014). Annual home range sizes of cougars in my population were slightly larger than in southern Alberta (140 km^2 for females and 334 km^2 for males; Ross and Jalkotzy 1992) and Arizona (114 km^2 for females and 326 km^2 for males; Nicholson et al. 2014), and larger compared to those in British Columbia, Canada and New Mexico, United States where adult female and male home range size were 55 km^2 and 151 km^2 and 74 km^2 and 187 km^2, respectively (Spreadbury et al. 1996, Sweanor et al. 2000). In British Columbia and New Mexico, cougars were not harvested. Therefore, I suggest that the larger home range sizes in my study area is related to harvest. Similarly, Maletzke et al. (2014) reported that cougars in a hunted population had larger home range sizes compared to a non-hunted population. In my study area, the high turnover of cougars from harvest and other human-caused mortality probably lowers cougar population density, creating more available habitat that results in larger annual home ranges, and leaving a vacancy for neighboring individuals or dispersers to fill (Nagy and Haroldson 1990).

I found that annual home range sizes were not significantly different between subadult males and females, however, they were larger for adult males compared to adult females by approximately 2.8 and 2.5 times for MCP and BBHR, which is consistent for adult males (range 1.5 to 3 times larger) in cougar studies throughout their distribution (Belden et al. 1988, Ross and Jalkotzy 1992, Spreadbury et al. 1996, Sweanor et al. 2000, Logan and Sweanor 2001, Grigione et al. 2002, Maletzke et al. 2014). In contrast to my results, Franklin et al. (1999) found male and female home ranges in Patagonia were similar in size. Females are expected to occupy a home range that will maximize breeding success and can provide adequate stalking cover, protection from predators, opportunity to become familiar with neighboring cougars (Pierce et al. 2000), and most importantly sufficient prey (Sandell 1989). Males have a larger body size than females and require more food. However, females must provide for their young for one to two years and as a family can have approximately 3 times the metabolic requirement of an adult male (Logan and Sweanor 2010), thus it is unlikely that food alone explains the larger male home range size. Adult male cougars increase breeding success by defending a territory that generally intersects multiple female home ranges (Sandell 1989). With no direct contribution to raising offspring, males can patrol a larger area in search of prey, estrous females, and to defend against invading males (Logan and Sweanor 2001, Dickson and Beier 2002).

2.4.2 Space Use Patterns

Some of the four space use patterns I found were more common than others. Dispersers were all subadults and primarily young males with a few females, however the space use one year post-capture was approximately fourteen-times larger for males than females (Table 2.2).

Dispersal by juvenile males from the natal range is a common mammalian pattern (Greenwood 1980). Male cougars almost always disperse greater distances away from their natal range to avoid inbreeding and is independent of male density (Seidensticker et al. 1973, Logan and Sweanor 2001). In my study one subadult male was philopatric after his mother died and sister dispersed. Similar behavior occurs in leopards (*Panthera pardus*) where subadult males were opportunistically philopatric and dispersal distance increased with increasing population density and adult male density (Fattebert et al. 2015). The subadult females in my study were largely philopatric, which helps to establish matrilineal assemblages where related females may have more tolerance for each other during resource competition (Greenwood 1980, Sweanor et al. 2000). Similar findings occurred in Eurasian lynx (*L. lynx*) and leopards where females typically remained philopatric and formed matrilineal assemblages (Fattebert et al. 2015, Holmala et al. 2018).

Adult cougars in my study had one of three space use strategies with the majority being residents (65% females, 56% males), followed by shifters (22% females, 33% males), and seasonal shifters (13% females, 11% males). The dynamic patterns observed are probably influenced by prey and mate availability, safety, such as cover that will provide refuge from predators, population density, and how cougars respond to changes in time and space of these factors. A seasonal climate and heterogeneous habitat likely affects prey distributions across the study area. Seasonal variability occurs in semi-arid or temperate ecosystems and prey aggregate to areas with higher forage or water (Western 1975, Boyce 1991). In such ecosystems, the distribution of large carnivores mirrors their prey distribution (Trinkel et al. 2004, Davidson et al. 2013, Johansson et al. 2018). Johanssen et al. (2018) documented a seasonal shift in cougar home ranges as they followed elk to their wintering habitat. In regions where agriculture is more prevalent, deer, the primary source of prey for cougars in my study area (unpublished data), cluster to take advantage of high quality forage and cover during winter months (Telfer 1978). The eastern portion of the study area is largely forested habitat that borders agricultural land. Two seasonal shifting cougars had home ranges bordering farmland and shifted their range to utilize areas along agricultural fields in autumn, suggesting the shift was driven by prey availability. Where large patches of homogenous habitat occur, prey density may be similar throughout. If an individual is able to kill enough prey within its home range to meet energetic demands it may be beneficial to being a resident and utilize familiar habitat.

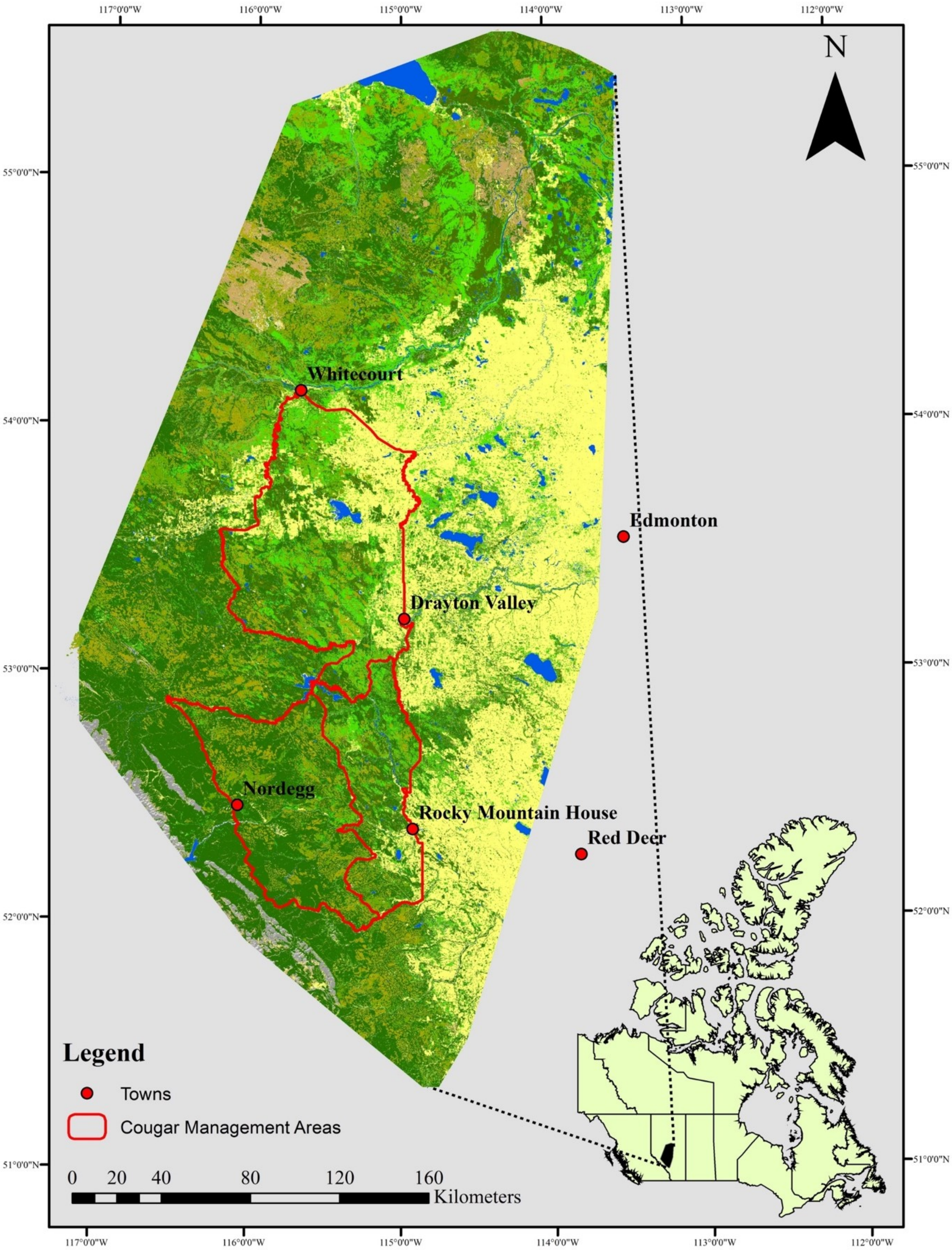
Mate availability is believed to be a primary driver of male space use in solitary large carnivores, with individuals using the landscape to maximize their breeding opportunities (Macdonald 1983, Sandell 1989, Goodrich et al. 2010). Female cougars are found in low densities and are aseasonal breeders (Logan and Sweanor 2001). Males usually have a home range that overlaps with multiple females and frequently check scent posts for females in estrous and are vigilant in defending against intruding males (Logan and Sweanor 2001). Having high home range fidelity likely allows resident males to gain knowledge on the location of adult females overlapping their home range, increasing the likely-hood of contact with estrous females and breeding success. Clutton-Brock (1989) suggested that males of many mammals focus their space use to an area inhabited by a fertile female, guarding her against other resident males. Although this behavior has not been documented in cougars, similar patterns have been observed in snow leopards (*P. unica*) where males reduced their home range size during the breeding season while females did not (Johansson et al. 2018). Although discussion on the effects mate availability has on space use tends to be male focused (Sandell 1989, Kovach and Powell 2003), female mate selection has been observed in large carnivores and may affect their space use

(Gottelli et al. 2007). Most females in my study had a home range that overlapped with multiple male cougars (Figure 2.4). By intersecting their home range with multiple males, females have a choice of overlapping males to mate with (Johansson et al. 2018). In regions where male mortality is high, infanticide is a primary cause of death of cougar kittens (Cooley et al. 2009, Ruth et al. 2011, Wielgus et al. 2013). To reduce the risk of infanticide, solitary large carnivore females may mate with multiple neighboring males to form cordial relationships and confuse males of paternity (Logan and Sweanor 2001, Balme et al. 2013). Therefore, females may benefit by remaining in a familiar area and can maintain amicable relationships with nearby males.

Cougar density may also contribute to dynamic space use patterns. High densities likely increase competition between resident males and immigrating subadult or neighboring territorial males (Logan and Sweanor 2001). Direct challenges can result in range expansion if victorious and range loss if defeated and has been observed in tigers (*P. tigris*) (Smith 1993) and leopards (Norton 1987). Females may respond to high densities by reducing fidelity to their range, resulting in a space use pattern that would enable them to avoid unfamiliar cougars, especially males which may commit infanticide (Ruth et al. 2011). At low densities, individuals could shift their range to utilize higher quality habitat when vacancies are available. In my study area, harvest of both sexes results in habitat becoming available. Spreadbury et al. (1996) found that an adult female cougar shifted her range into an area vacated by a neighboring adult female and similar findings have been observed in Ethiopian wolves (*C. simensis*) (Zubiri and Gottelli 1995). If the vacant area provides hunting opportunity and escape from predators or aggressive cougars, it may be beneficial for females and their offspring to shift their home range. Death of an adult male will create a vacancy that intersects multiple adult female ranges. The vacancy can provide opportunity for immigrating subadult males to establish a high-quality home range, or neighboring adult males to shift their range to encompass the females within the vacancy.

Increased knowledge of the different space use patterns used by individuals within a population will help in understanding social stability and population structure. Given the dynamics of cougar space use, I believe harvest plays a significant role in creating habitat vacancies. The methods I used to distinguish the different space use patterns of cougars could be applied to other studies investigating home range patterns to better understand the variability in space use. Similar analysis could be applied to a variety of species, both migratory and non-migratory. Documenting space use, however, is one aspect of understanding autecology but larger challenges remain in explaining why they occur.

Figures



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Rocky Mountain House
Red Deer
Legend
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Cougar Management Areas
0 20 40 80 120 160
Kilometers

Figure 2.1 The study area in west-central Alberta, Canada, showing the Cougar Management Areas where cougars were captured, and collared. The study area was defined using a 100% minimum convex polygon (MCP) around all cougar locations used in the analysis.

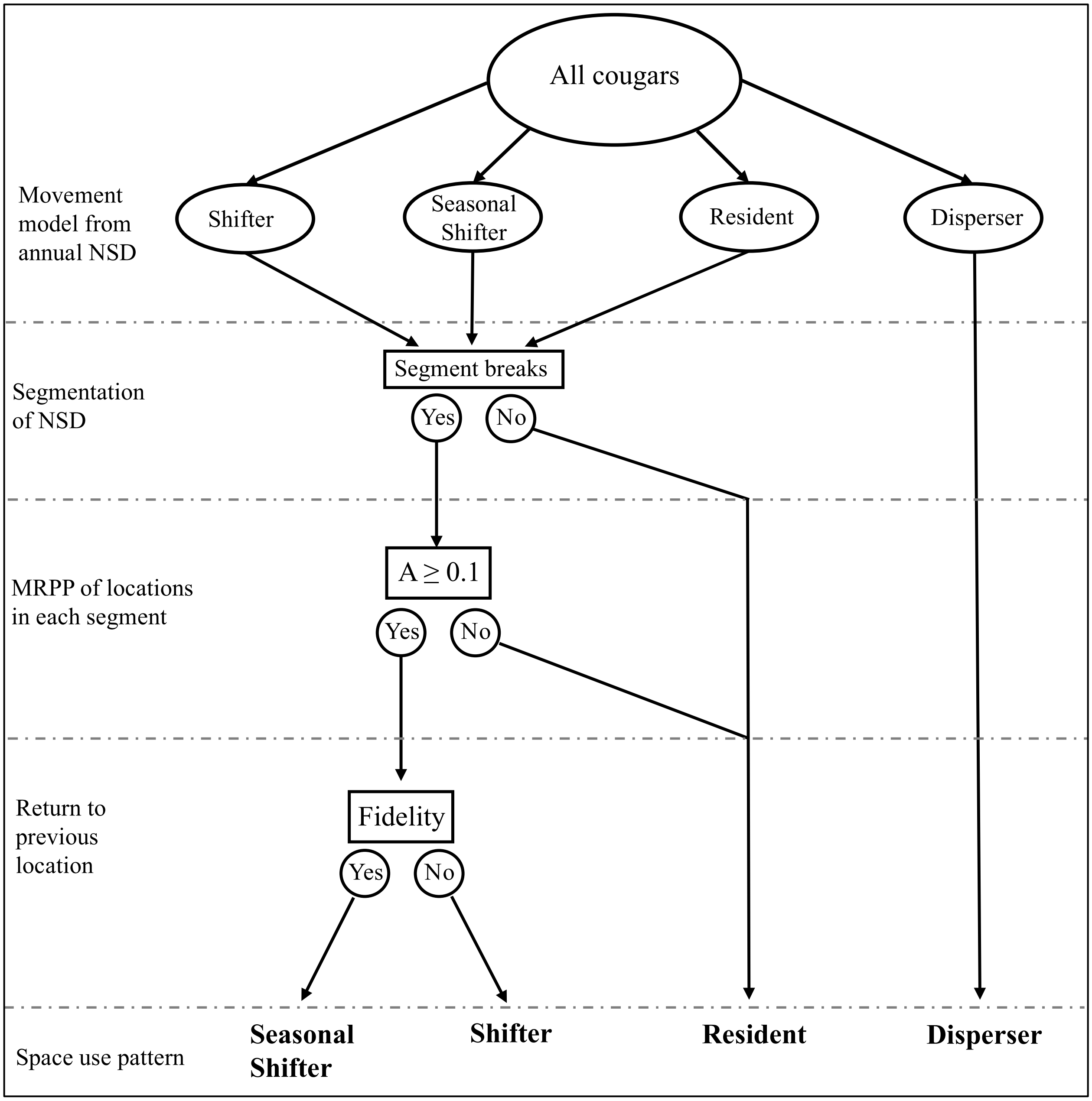

Figure 2.2 Decision tree using 3 analyses to categorize cougars into space-use strategies. The first analysis uses Akaike information criteria (AIC) to fit annual net squared displacement (NSD) of each

individual into 1 of 4 nonlinear movement models. The second analysis found breaks in the animal's track (Lavielle 1999, 2005). The third method used a Multi Response Permutation Procedure (MRPP) to determine if X and Y coordinates of path segments, as determined from breaks, were different from one another.

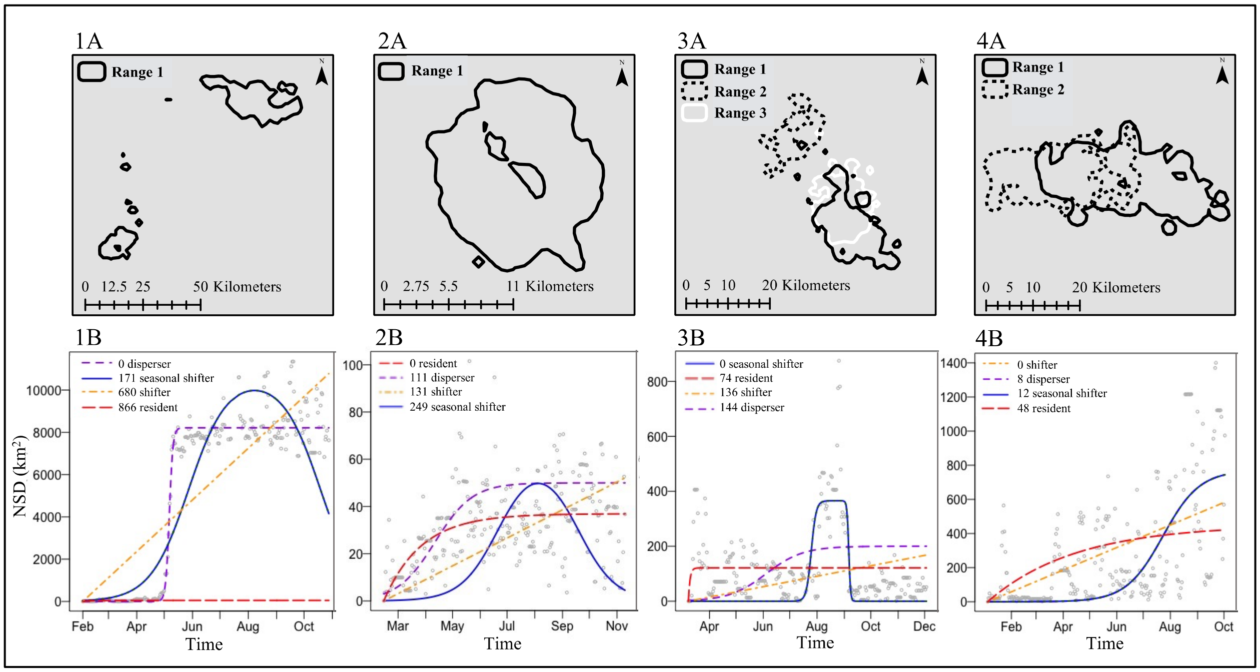

Figure 2.3 Examples of four identified space use patterns and their range shifts for four cougars collared between 2016-2018 in west-central Alberta, Canada. Figure shows the 95% Brownian Bridge Home Range (BBHR) for 1A – a disperser, 2A – a resident, 3A – seasonal shifter, and 4A a shifter. Panel (B) showing the net squared displacement (NSD) for the same four cougars and their fit to the modified movement models used based on models used in migrateR and the ΔAIC scores for each model. Panel B represents the first analysis in identifying the space use strategy used by each cougar and is followed by the segmentation analysis and Multi Response Permutation Procedure (MRPP).

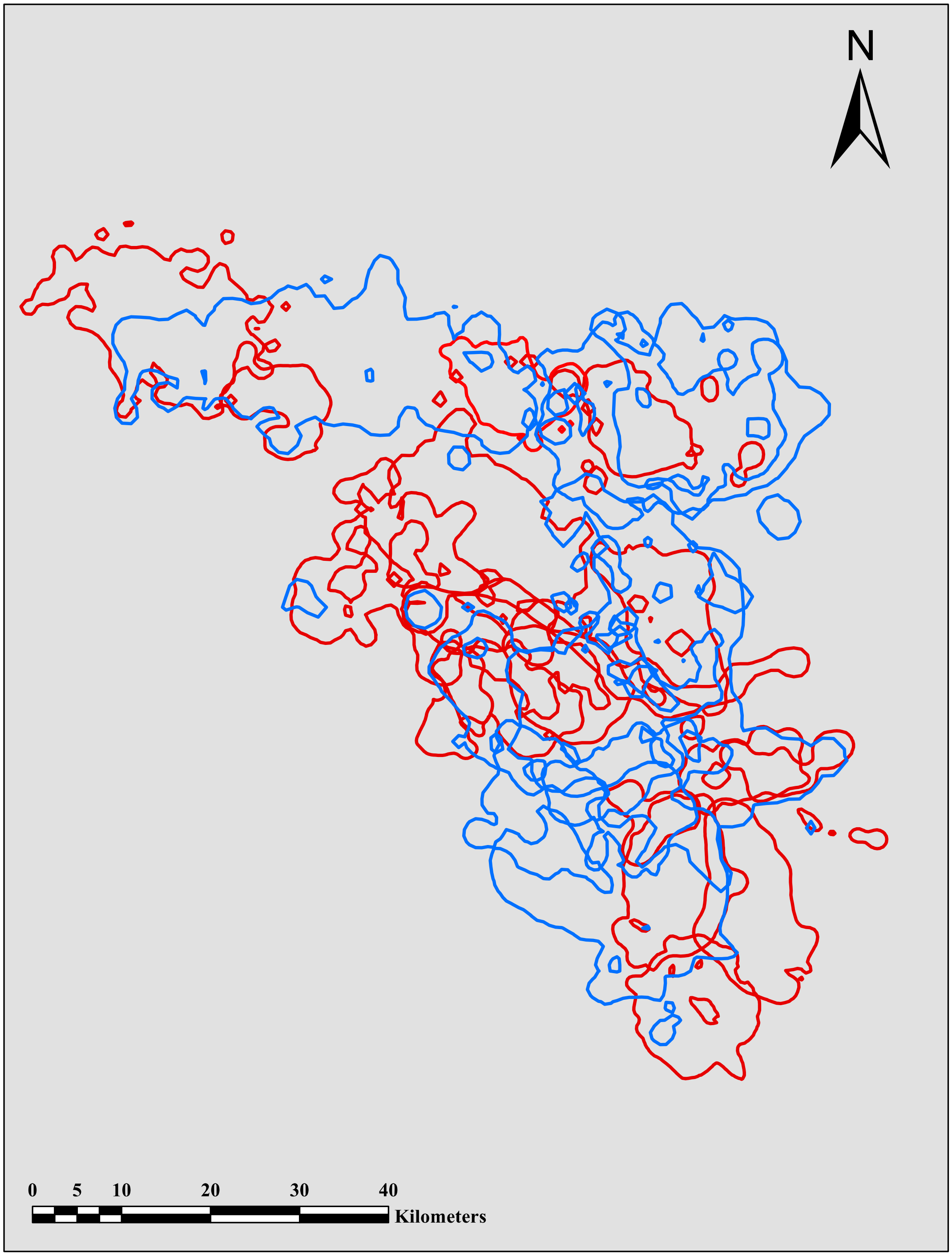

Figure 2.4 95% Brownian Bridge Home Ranges of male (blue) and female (red) cougars in west-central Alberta, Canada.

Table 2.1 The annual (270 days) 95% Minimum Convex Polygon and Brownian Bridge Home Range estimates (+/- SE) for 43 adult and subadult cougars captured in west-central Alberta from 2016 – 2018.

Group	MCP (km^2)	MCP range (km^2)	BBHR (km^2)	BBHR range (km^2)	n
Subadult female	518 ± 274	121 - 1043	467 ± 190	191 - 832	3
Subadult male	6153 ± 2255	152 - 17709	1515 ± 392	203 - 2944	8
Adult female	181 ± 23	39 - 499	217 ± 18	79 - 422	24
Adult male	498 ± 75	498 - 902	547 ± 84	252 - 1021	8

Table 2.2 The annual 95% Minimum Convex Polygon (MCP) and Brownian Bridge Home Range (BBHR) estimates (+/- SE) for 42 cougars categorized into the 4 defined space use patterns using a decision tree, migrateR, track segmentation analysis and Multi Response Permutation Procedure. One cougar was not included because it had an undefined space use pattern.

Space use pattern	MCP (km^2)	Range MCP (km^2)	BBHR (km^2)	Range BBHR (km^2)	n
Disperser					
Female	518 ± 274	(121 – 1043)	467 ± 190	(191 – 832)	3
Male	7010 ± 2408	(918 – 7709)	1703 ± 397	(582 –2944)	7
Resident					
Female	142 ± 14	(39 – 259)	186 ± 13	(79 – 285)	15
Male	497 ± 123	(152 – 902)	579 ± 134	(203 – 1021)	5
Seasonal shifter					
Female	216 ± 116	(65 – 445)	244 ± 90	(117 – 419)	3
Male	321 ± N/A	N/A	331 ± N/A	N/A	1

Shifter					
Female	211 ± 42	(67 – 310)	254 ± 42	(110 – 364)	5
Male	443 ± 123	(210 – 629)	453 ± 109	(252 – 626)	3

Table 2.3 Summary of the analyses used to determine space-use strategy of 43 cougars and their 95% Brownian Bridge Home Range (BBHR) and Minimum Convex Polygon (MCP) annual home range size. Annual Net Squared Displacement (NSD) was used in the first analysis to categorize space use patterns, the second analysis used segment breaks to determine if cougars had shifts in their annual home range. "A" represents the chance corrected, within-group, agreement statistic and is the result of the Multi Response Permutation Procedure. Annual home range estimates were standardized to 270 days and space use patterns were based on that time period at one/location a day.

Animal Id	Sex	Age	Annual NSD Model (270 days)	Segment Breaks	A	Space Use Pattern (270 days)	95% MCP (km^2)	95% BBHR (km^2)
F3	F	1.2	Disperser	No	-	Disperser	391	378
F32	F	1.5	Disperser	No	-	Disperser	1043	832
F33	F	1.5	Disperser	No	-	Disperser	121	191
M3	M	2	Disperser	No	-	Disperser	17709	2944
M4	M	2	Disperser	No	-	Disperser	1143	582
M6	M	2	Disperser	No	-	Disperser	12822	2824
M9	M	2	Disperser	No	-	Disperser	8777	2617
M13	M	2	Disperser	No	-	Disperser	918	789
M21	M	1.5	Disperser	No	-	Disperser	3297	838
M22	M	1.5	Disperser	No	-	Disperser	4404	1325
F19	F	2	Resident	Yes	0.04	Resident	225	240
F42	F	2.5	Resident	Yes	0.03	Resident	39	79
F28	F	6	Resident	Yes	0.02	Resident	148	197
F2*	F	2.5	Resident	No		Resident	110	177
F46	F	5	Resident	Yes	0.05	Resident	150	209
F1*	F	3	Resident	No	-	Resident	172	188
F18	F	6	Resident	No	-	Resident	150	214
F23	F	2.5	Resident	No	-	Resident	118	170
F30	F	9	Resident	No	-	Resident	155	200

F39	F	7	Resident	No	-	Resident	148	198
F44	F	2.5	Resident	No	-	Resident	259	285
F26	F	7	Resident	No	-	Resident	55	102
F37	F	6	Resident	No	-	Resident	141	187
M8	M	5	Resident	Yes	0.05	Resident	441	555
M2	M	5	Resident	No	-	Resident	902	1021
M5	M	3	Resident	No	-	Resident	407	450
M1	M	0.8	Resident	No	-	Resident	152	203
M16	M	5	Resident	No	-	Resident	582	660
F9[*]	F	6	Seasonal Shifter	Yes	0.08	Resident	108	145
F34	F	4	Resident	Yes	0.09	Resident	158	193
F41	F	1.5	Resident	Yes	0.19	Seasonal Shifter	65	117
F45	F	4	Seasonal Shifter	Yes	0.27	Seasonal Shifter	138	196
F36	F	3	Seasonal Shifter	Yes	0.36	Seasonal Shifter	445	419
M11	M	3	Seasonal Shifter	Yes	0.12	Seasonal Shifter	321	331
F38	F	6	Shifter	Yes	0.11	Shifter	67	110
F25	F	7	Resident	Yes	0.12	Shifter	213	266
F6	F	3	Shifter	Yes	0.12	Shifter	310	364
F21	F	5	Shifter	Yes	0.17	Shifter	187	227
F15	F	2.5	Shifter	Yes	0.4	Shifter	279	301
M7	M	3	Shifter	Yes	0.13	Shifter	490	482
M10	M	3	Shifter	Yes	0.27	Shifter	210	252
M14	M	5	Shifter	Yes	0.16	Shifter	629	626
F16	F	3	Resident	Yes	0.27	Undefined	499	422

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Chapter 3

3 Seasonal habitat selection of cougars (*Puma concolor*) by sex and reproductive state in west-central Alberta, Canada

3.1 Introduction:

Understanding how animals use the environment to acquire resources crucial to their survival is fundamental in wildlife management and conservation. A common method used in assessing the relationship between animals and their environment are resource selection functions which use a use versus unused or use versus availability framework to assess habitat characteristics which are selected or avoided on the landscape (Boyce et al. 2002, Manly et al. 2002). Terrestrial carnivores tend to be secretive and live in low densities, making habitat selection studies difficult without the use of telemetry data. Carnivore density is ultimately driven by prey abundance (Carbone and Gittleman 2002), however habitat features such as vegetation, travel corridors and human disturbed habitat may influence the quality of habitat, and therefore the encounter rate with prey. Understanding habitat selection for large carnivores can provide insights into the resources needed for their survival and inform industry and management on regions that may be important for species conservation.

Cougars (*Puma concolor*) are the widest ranging mammal in the western hemisphere, with populations extending to northern British Columbia and south to Chile (Yáñez et al. 1986, Walker et al. 2010, Teichman et al. 2013, Sunquist and Sunquist 2017). They occupy ecosystems as varied as the desserts of southwestern United States and northern Mexico, temperate rainforests, and harsh winter areas of the western Canadian provinces (Ross and Jalkotzy 1992, Logan and Sweanor 2001, Sunquist and Sunquist 2017, Elbroch and Kusler 2018). The main habitat requirements for cougars are availability of large prey, cover such as thick vegetation for concealment, and areas exempt from major human development and disturbance (Seidensticker et al. 1973, Koehler and Hornocker 1991). However, cougars are flexible within these requirements as they have high prey plasticity (Soria- Díaz et al. 2018), exploit a diversity of ecosystems (Berger and Wehausen 1991, Núñez et al. 2000), and live in areas with fragmented habitat and human-caused mortality (Knopff et al. 2014a).

At a finer scale, cougars tend to hunt prey, have rest areas and raise their offspring in landcover types with a thick understory (Maehr and Cox 1995, Dickson and Beier 2002). In many regions, cougars coexist with other predator species (Elbroch and Kusler 2018), and selection for dense forested vegetation may reflect avoidance of dominant carnivores instead of selection of high quality habitat (Durant 1998). Within forested habitat, cougars tend to use locations closer to open landscapes and wetlands which are likely used by prey, and the transition between habitat types provide good stalking cover (Dickson and Beier 2002, Laundré and Hernández 2003, Cox et al. 2006, Knopff et al. 2014a). Cougar habitat selection varies, but they tend to prefer steep terrain and riparian areas which may provide a hunting advantage (Logan and Irwin 1985, Dickson and Beier 2002). Cougars avoid open terrain, areas of high paved road density, and habitat disturbed by humans (Van Dyke et al. 1986, Dickson and Beier 2002, Arundel et al. 2003).

The habitat an animal selects may be influenced by sex and reproductive status, and evaluation of species habitat selection should incorporate these factors (Benson and Chamberlain 2007). Like many animal species, female cougars spend most of their adult life pregnant or raising offspring and require high quality habitat that will provide them with sufficient resources as they care for their offspring (Logan and Sweanor 2001). In contrast, males do not contribute to offspring rearing and instead invest their energy in traversing their home range in search of estrous females and defending against intruding males (Logan and Sweanor 2001, Dickson and Beier 2002). Therefore, habitat selection may differ between male and female cougars. Furthermore, because of decreased mobility of females with offspring and increased nutritional demand (Logan and Sweanor 2001), differences in habitat selection between female large carnivores with and without offspring can be expected (Benson and Chamberlain 2007). Until approximately 6 - 8 weeks old, cougar kittens are dependent on the safety of a nursery site and unable to travel with their mother (Logan and Sweanor 2001), restricting the mother's movements to areas near the nursery site (Elbroch et al. 2015). As the kittens age, they begin travelling with their mother and become more nutritionally demanding and the mother may need to make a kill multiple times a week (Logan and Sweanor 2009). In comparison, solitary cougars may only need to kill once a week depending on the size of prey, can generally defend against or escape other predators, and are unconstrained by offspring mobility (Logan and Sweanor 2001).

In temperate ecosystems, habitat features that are selected for or avoided can change seasonally. Deep snow can make travelling on steep slopes or higher elevations energetically demanding and avoidance of these regions may be beneficial to cougars in winter months (Koehler and Hornocker 1991). Prey may also move to lower elevations or habitat to forage and cougars may follow prey and use different habitat types seasonally (Telfer 1978, Koehler and Hornocker 1991). Numerous studies investigating cougar habitat selection found that cougars tend to use edge habitat, riparian areas, forested landcover, and sloped and rugged terrain, while avoiding close proximity to roads and other anthropogenic disturbances, and open terrain (Logan and Irwin 1985, Van Dyke et al. 1986, Belden et al. 1988, Dickson and Beier 2002, Knopff et al. 2014a). However, few studies have investigated how habitat selection is affected by season or sex and reproductive state of the individual.

I studied habitat selection of cougars in west-central Alberta, Canada with the primary goal of determining habitat selection at the home range scale and then, using the results of a two-step resource selection function (RSF), determine what the most important habitat features are for independent adult males, adult females, and reproductive females for winter and summer at the population level. I predicted that cougars will: 1) use areas within their home range where hunting success would be high such as edge habitats or areas closer to water, 2) select complex habitats that provides protection from competing carnivores as well as hunting opportunity such as forested habitats and sloped or rugged terrain, 3) avoid anthropogenic features such as roads, human-use areas, and natural resource extraction areas, 4) the most important habitat features for females with kittens will be areas where hunting success and safety will be highest, 5) important habitat for single females and males will be similar, and 6) importance of habitat features will change seasonally for all groups.

3.2 Methods

3.2.1 Study Area

The study occurred in west-central Alberta, Canada from 2016 to 2018 (Fig 1) and covered ca. 26,205 km^2. The area is in the central mixed-wood, lower foothills, upper foothills, subalpine, and alpine ecoregions (Natural Regions and Subregions of Alberta. 2006). Logging and hydrocarbon extraction activities are common and have created a network of roads, pipelines, and seismic lines. The study area was west of the town of Rocky Mountain House and extended north to Whitecourt, south towards Sundre and borders the Rocky Mountains to the west. The area transitions from agricultural lands to the east with rolling foothills and eventually mountains to the south and west, with boreal habitat to the north. The dominant forest type of the region are coniferous stands of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*), while black spruce (*P. mariana*) and tamarack (*Larix laricina*) occur near wetlands or lower elevations (Government of Alberta, 2011). Broadleaf and mixedwood forests are more common in the north and east and contain balsam poplar (*Populus balsamifera*) and aspen (*P. tremuloides*). The climate is highly variable and has cold winters with heavy snow falls, wet springs, and warm summers (Strong 1992). Cougar hunting occurs from autumn to late winter in Alberta and the study area covered three cougar management areas (CMAs 11, 12, and 21). Cougar populations have expanded east since the early 1990s (Knopff et al. 2014b). The expanding population and encroachment of people into cougar habitat has resulted in increased human-cougar conflict.

Large prey in the region include white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), moose (*Alces alces*), elk (*Cervus elaphus*), and feral horses (*Equus caballus*). Cougars may also prey on bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*), however both are less abundant in the region. Small prey include snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), red fox (*Vulpes vulpes*), ruffed grouse (*Bonasa umbellus*), and spruce grouse (*Falcipennis canadensis*). Cougars in the region may prey on domestic animals. A number of other predators are found in the area and include black bears (*Ursus americanus*), grizzly bears (*U. arctos*), lynx (*Lynx canadensis*), wolves (*Canis lupus*), coyote (*C. latrans*), and wolverine (*Gulo gulo*).

3.2.2 Cougar Capture

Cougar habitat use data was obtained from cougars that were captured and fitted with global positioning system (GPS) radiocollars from 2016 - 2018. Cougars were caught using snow tracking and trained hounds to tree animals. Treed cougars were immobilized by remote injection using a drug combination of Telazol® (1.7-2.6 mg/kg) and Medetomidine (0.05 - 0.075

mg/kg). Once processing was complete cougars were reversed using Atipamezole (0.4 mg/kg) (Government of Alberta). Vectronics Vertex Lite VHF/GPS radio collars were fit on cougars and recorded a GPS location every 4 hours for females and 7 hours for males and were retrieved via Iridium satellite (Vectronic Aerospace, GmBh, Berlin, Germany). Collars were recovered after harvest, recapture, or when the 2-3-year cotton rot-away broke down and the collar fell off the cougar. Age was estimated using gum-line recession, pelage spotting and barring and tooth color and wear (Laundré et al. 2000, Heffelfinger 2010). All procedures followed the Alberta Wildlife Animal Care Committee Class Protocol #12 (Research Permit 5986) and were consistent with the Canadian Council on Animal Care. Though immobilization and capture procedures may affect animal movement patterns (Thiemann et al. 2013), no study has investigated post-capture effects on cougar movement patterns or habitat use. Therefore, similar to Thiemann et al. (2013), I removed the first 5 days of location data to reduce the effects of handling on habitat use in my analysis.

3.2.3 Cougar Data Preparation

Only cougars that had an established home range were used in the analysis and dispersing animals were excluded. Home range establishment was identified using segmentation analysis (Lavielle 1999, Smereka et al. unpublished data, Chapter 2) as well as visual inspection. The segmentation analysis identified homogenous bouts of mean and variance of the cougars Net Squared Displacement (NSD) with changes in mean and variance resulting in individual track segments. If no breaks occurred in a track the individual was determined to have established a range. To verify the results of segmentation analysis, range establishment was also visually identified as the time at which unidirectional movements away from the natal range stopped and the animal began to reuse an area. The GPS points corresponding to the range establishment were the use points. Some individuals went on long excursions away from their home range and these excursions were deleted from the use locations as I did not consider them part of the individual’s home range.

Adult cougars were grouped by sex and by reproductive status: male, single female, and female with offspring. Groupings for females were based on evidence of kittens at the time of collaring and follow up ground surveys, camera traps at kill sites, and nursery site visits. Once kittens dispersed, females were categorized as single females. I only used females of known reproductive status. I split use points into periods when snow is on the ground and temperatures were typically below freezing (November 1 to March 31), and green-up and waterbodies thaw and open (April 1 to October 30) (Girard et al. 2013). These two periods are referred to as winter and summer, respectively. Cougar use data was also split into reproductive status and season, resulting in six total groups: males in winter (MW), males in summer (MS), single females in winter (SFW), single females in summer (SFS), females with kittens in winter (KW), and females with kittens in summer (KS).

3.2.4 Habitat Covariates

To investigate habitat selection, I included four types of variables which could be important to cougars in Alberta: land cover, topography, prey, and human disturbance (Table 3.1). Land cover data was obtained from the Canadian Service Earth Observation for Sustainable Development of Forest (EOSD) from 2000 from Landsat data and has a 25m pixel resolution (Natural Resources Canada 2009). I used the Alberta Biodiversity Monitoring Institute’s human footprint index (HFI) layer (Alberta Biodiversity Monitoring Institute 2012b) to update the EOSD landcover layer with forestry and hydrocarbon extraction activity and road development to match the study period. The HFI layer provides an updated Alberta wide representation of anthropogenic activity. The land cover dataset was reclassified into nine ecologically relevant land cover types for cougars including: old cutblocks (>25 years old), recent cutblocks (≤25 years old), industrial (roads, well sites, compressor stations), barren (exposed land, rock/rubble), shrub, wetland (herb, shrub, and treed wetland classes dominated by black spruce), open agricultural land, conifer forest, and mixed deciduous forest (broadleaf and mixedwood forest). Water was not considered available habitat for cougars and was not included in models. Cut-block categorization was based on vegetation regeneration stages (Song 2002).

Topographic variables included: elevation, slope, terrain ruggedness index, distance to water, and distance to edge habitat. I used a 25 m digital elevation model (DEM) (AltaLis, accessed 2019) and Spatial Analyst in ArcGIS [Environmental Systems Research Institute (ESRI) 2008, Redlands, CA, USA] to develop layers for elevation, slope, aspect, and terrain ruggedness index (TRI). Elevation for each pixel was obtained directly from the DEM. Slope was calculated by determining the maximum difference in elevation between the central pixel and its eight neighbouring pixels. TRI measures the elevation change between a pixel of the DEM and its eight neighbouring cells and I used this to measure terrain heterogeneity. Forest edge was defined as the intersection between forest land cover types and the Euclidean distance from each pixel to forest edge was calculated to create the distance to edge layer. I created a distance to water layer by calculating Euclidean distance from each cell to water. It is likely that locations close to forest edge or water have more of an effect on cougars compared to locations further away, therefore I also derived exponential decay layers for both edge and water. Exponential decay layers are formed using the function ($e^{(-d/\alpha)}$), where d uses the distance-to layers and α was set to the buffer for the scale of selection (Nielsen et al. 2009). I created multiple exponential decay layers for forest edge and water based on the literature and field observations and used buffer radii of 30, 50, and 100 m (Croonquist and Brooks 1991, Holmes and Laundré 2006, Knopff et al. 2014a).

I used data collected from scat counts to create probability of occurrence layers to include as prey indices in my cougar RSF. Scat counts were conducted from May to June in 2018 and 2019. I searched 2 m wide by 1.5 km long transects for scat from deer, moose, elk, horse, hare, grouse or any other prey available to cougars in the study area. A GPS location of each scat along with species identification and land cover type were recorded. If more than half of the scat group was outside the transect it was not recorded. Five random locations were generated for each scat location within a buffer the radius of the species home range. I used a backward elimination procedure using stepAIC in the MASS package in R (Venables and Ripley 2002) to create use versus availability layers for each of the prey species. I evaluated the predictive capacity of the prey models using a k-fold cross validation where models were trained using 80% of the data and tested using 20% of the data (Boyce et al. 2002).

I used road, wellsite, compressor site, pipeline, and residential data obtained from the HFI to create habitat disturbance layers by calculating the Euclidean distance from each pixel to the nearest feature. I created distance to road, residential, extraction (active wellsites and compressor stations) and also used these rasters to create exponential decay layers for road (170 m), residential (210 m), and extraction (100 m) (Knopff et al. 2014a). Layers were created in ArcGIS using the distance tool and raster calculator.

3.2.5 Habitat Selection

Habitat features that may influence resource selection of cougars of different groups were assessed using a resource selection function (RSF) in the exponential form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 \dots \beta_k x_k)$$

where *w(x)* is the RSF, x_i are the habitat variables and β_i are the corresponding selection coefficients (Manly et al. 2002). Used locations were cougar GPS fixes.

Before modelling, available points were generated at a density of 10 points/km^2 within a cougar's 100% minimum convex polygon (MCP) in ArcGIS using the Minimum Bounding Geometry tool to calculate the habitat available to each cougar (i.e., third order; Johnson 1980). I considered the MCP a suitable measure of availability as it represented each individual's home range, and for my study animals, did not include large areas of unused habitat after visualization of the location data. All use and available points were mapped on a 25 m grid and had habitat attributes extracted in ArcGIS. Use locations for each individual within a group were compared to the available locations within their total home range to determine what habitat variables were selected or avoided depending on season and reproductive status of the individual. Where locations were on water but close to land, and because distance to water was included in my analyses, I decided to keep the data in my analysis after snapping it to the nearest non-water landcover type. The majority of the locations on water occurred during the summer, therefore I believe cougars were using areas adjacent to water. Locations on water could be due to GPS location fix error (5-10 m) or because many of the streams in the study area are not as wide as the cell grid size and cougars travelling along a stream edge may have GPS fixes within the water pixel.

Because covariates in my models were either binary (i.e., landcover types) or continuous (i.e., slope), I standardized each continuous predictor variable so it had a mean of 0 and standard deviation of 1 before analysis (Gotelli and Ellison 2004). Each continuous variable was checked for nonlinear fit (i.e., quadratic or natural log transformation) and the form with the lowest AICc was used in the models. For distance-to variables that also had exponential decay forms, only the layer with the best AICc fit was kept for analysis. Before analyses, collinearity was assessed between variables and variables that had a Pearson's correlation coefficient of $\geq |0.6|$ were not included in the same model. I also tested the variance inflation factor (VIF) of variables in each model and if the VIF > 3 for any variables the variable with the highest VIF was removed from the model. VIF was checked for each model until there were no variables with a VIF >3. For the habitat model, the landcover reference category used was conifer forest (CF) as it was the most common and widely distributed across the study area. Shrub (SB) and barren (BN) landcover types make up <1% of the available points, and are likely to result in perfect predictors (outcome variable completely separates the predictor), therefore SB and BN were not included in the analyses and grouped into the reference category.

I used two RSF methods to analyze cougar habitat selection at the home range scale (Johnson 1980); a mixed-effects logistic regression model (Gillies et al. 2006) and a two-step approach (Fieberg et al. 2010). Mixed-effects models can be computationally demanding, difficult to interpret, and may have over-optimistic estimates of standard errors, however, because my modelling approach was based on an *a priori* set of models, it allowed us to find the top model describing cougar habitat selection among the six groups, and identify a single model that could be used in the two-step approach. I used the package *lme4* in R to construct and analyze six *a priori* models (Table 3.2) (Bates et al. 2007). Model construction was based on cougar habitat selection literature (Seidensticker et al. 1973, Logan and Sweanor 2001, Dickson and Beier 2002, Knopff et al. 2014a) as well as observations in the field that may be study area specific. Models for prey, prey habitat, natural habitat, anthropogenic features, safety, and a model with variables from each called "combined" were created. A random effect of animal ID was added to each model to account for autocorrelation and unequal sample sizes (Gillies et al. 2006). The six models plus the null model, which included animal ID, were tested for each grouping of cougars and the model with lowest AICc but > 2 ΔAICc from the top competing model was considered the top model (Burnham and Anderson 2002). I then included interaction terms in the top model if deemed suitable *a priori* and kept them in the model if the interaction was significant for each group.

The primary focus of my RSF analysis used the two-step modelling approach and was used to estimate population level habitat selection for the six groups. The two-step approach provides a method for dealing with autocorrelation, variability in number of use locations, and can fit a generalized linear model to individual animals (Fieberg et al. 2010). Due to the high variability in landcover type and terrain across the study area (Figure 3.1) and variability in sample sizes across individuals, I expected there to be high error rates for some coefficients (Takahata et al. 2014). For example, if sample size in a landcover type was highly variable among cougars, the reliability of a coefficient for individual cougars would not be equal. A way to deal with the disproportional error rates is to use an inverse variance weighted method (IVW), which incorporates differences in standard error of each parameter estimate to produce an appropriate population-level coefficient (Nielsen et al. 2009).

I used the package amt in R to fit the top model that was identified using the mixed effects regression to a glm for each individual in a group (Signer et al. 2019). I used bootstrapping with

4000 iterations to form 95% confidence intervals around the IVW mean to produce population level selection coefficients and determine the relative selection strength for each covariate (Avgar et al. 2017). Confidence intervals non-overlapping zero were considered significant for each beta-coefficient. I checked my results of the two-stage approach by determining if the averaged coefficients from the individual models that were significant, were consistent with results of the mixed effect model (i.e., predictor is significant and has the same sign of selection for both two-stage approach and mixed effects model), similar to Takahata et al. (2014) and Scobie et al. (2016).

3.3 Results

Seventy-two cougars were caught, however seven subadult males dispersed and left the study area and were excluded from the analysis as they may select habitat types differently than individuals with established ranges. Of the 65 cougars that remained in the study area, 10 females had an unknown reproductive status and were excluded from the analysis. There was a total of 58,432 use locations and 207,597 available locations for the 55 cougars retained for analyses. For MW there were 14 cougars (4,654 use locations, mean = 332, range = 54 - 655), MS there were 13 cougars (8,687 use locations, mean = 668, range = 101 - 958), SFW there were 32 cougars (12,822 use locations, mean = 401, range = 25 – 1,396), SFS there were 32 (23,547 use locations, mean = 736, range = 95 – 2,212), KW there were 13 cougars (4,608 use locations, mean = 316, range = 19 - 867), and KS 13 cougars (4114 use locations, mean = 354, range = 46 – 912).

Sixty-three random locations were generated in the study area and a total length of 184.5 km of transect was searched for prey scat. Pellet counts of prey only provided enough data to create probability of occurrence layers for deer and moose. K-fold cross validation produced a Spearman rank correlation that was low for moose ($r_s = 0.65$, $P = 0.09$), and high for deer ($r_s = 0.89$, $P < 0.001$), indicating the model for moose had a lower predictive success and the model for deer had a high predictive success. Of the use locations (1403 locations) 2% were located on water and snapped to the nearest landcover type. The natural log forms of TRI, SLOPE, DEXT and ELEV had the best fit, while the exponential decay forms of ED50, WAT100, RES210, and ROAD170 had the best model fit to cougar habitat selection. The deer RSF variable and conifer forest, as well as moose RSF and new cut-block were highly correlated and were not included in any of the same models.

The mixed effect RSF indicated that the combined model, which included SLOPE, WL, OAL, FOR, ED50, WAT100, RD170, and DEXT was the unanimous top model for all six groups of cougars and all had a model weight of 1 (Table A3.2-3.7.). I tested the interaction between RD170 and FOR as well as WAT100 and FOR, however, the interaction was only significant between RD170 and FOR in two groups and I therefore decided to leave out the interaction term to maintain simplicity in my top model.

Results of the two-step RSF of the combined model (Figure 3.2) indicate that the most important variables for cougar habitat selection across groups are edge habitat, close proximity to water, forested landcover, and slope which were selected (Figure 3.2, Table A3.1). However, selection for forested landcover and edge habitat was not significant for KS and selection for close proximity to water was not significant for KW. The six groups also avoided close proximity to road, although KS and KW were not significant. KS and MW also had significant selection for closer distance to oil/gas resource extraction.

Seasonally, males, single females, and females with kittens all had different variables that contributed the most to habitat selection (Table 3.3 – 3.5). In summer, the most important habitat feature for males was close proximity to water and wetland landcover, which were both significantly selected, while in the winter proximity to water and wetlands fell to the 3rd and last ranked variables (Table 3.3). During winter, numerous variables drove selection for males but the most important covariates were forested landcover and edge habitats, which were ranked 6th and 3rd most important during summer, respectively and both were selected. For single females in summer the most important variables were close proximity to water and forested landcover, that were both selected, while in winter both variables were ranked 3rd and 1st (Table 3.4). During winter the 2nd ranked selected variable was slope, which was the 4th ranked in summer, and both were significant. Large differences in magnitude of selection occurred for females with kittens (Table 3.5). During summer the most highly selected features were wetland landcover and closer proximity to water, which were both significantly selected and were the least important during winter. The highest-ranked features for females with kittens in winter were open agricultural land which was avoided, although insignificant, and forested landcover which was significantly selected. During summer open agricultural land and forested landcover were ranked 6th and 7th respectively and both were insignificant. Open agricultural land and distance to resource extraction were both highly variable for all groups.

All significant IVW coefficients from the two-step approach agreed with results of the mixed effect model (if significant for IVW was significant for mixed effect model and had the same sign of selection) (Table A3.1), however habitat that had lower availability had consistently larger selection coefficients in the mixed effects model compared to the IVW. Population level selection coefficients obtained from the two-stage approach for each season and reproductive status were mapped in ArcGIS to show regions of the study area with higher and lower relative selection (Figure 3.3). For single females and females with kittens in winter, the west and southwest region of the study area provides the highest-quality habitats (Figure 3.3; 1B and 2B), while in summer the study area has a similar quality habitat throughout (Figure 3.3; 1A and 2A). For males, relative selection is similar for both seasons with greater higher-quality habitat west (Figure 3.3; 3A and 3B).

3.4 Discussion

Habitat selection for cougars of all sex and reproductive status in summer and winter were best predicted by the combined model, indicating that no one variable type drives habitat selection, but instead a combination of variable types influence cougar space use. My top model contained variables important for safety and visibility during hunting (SLOPE), related to anthropogenic disturbance (DEXT and RD170), prey and habitat (WL, OAL, WAT100, ED50, and FOR) and were consistent with my predictions that these variables would be important for each group. Although prey (DEER and MOOSE) were not in the top model, I believe habitat features that were selected reflect areas where prey were likely to occur or were more vulnerable to predation. A larger sample size of pellet count data or higher quality prey data (e.g., telemetry data or RSF throughout the year) may be required to create a layer that better represents areas of high prey availability.

Areas closer to edge habitat were consistently selected for by all groups of cougars, although not significant for females with kittens in summer. Forest edge is important for many carnivores (Šálek et al. 2014, McCarthy et al. 2015, Thapa and Kelly 2017) including cougars (Cox et al. 2006, Holmes and Laundré 2006, Knopff et al. 2014a). Cougars are not adapted for long distance pursuit of prey and instead rely on camouflage and sufficient cover to approach unsuspecting prey to a distance where a short burst of speed can be used to make a kill (Murphy and Ruth 2009). The transition from dense forested areas to more open terrain that occurs in edge habitat probably provides cougars with higher hunting success compared to homogenous forested habitat. Laundré and Hernández (2003) found that kill sites of mule deer were 2.5 times more likely to occur within 20 m of edge habitat compared to what was available. In my study area, broadleaf, mixedwood and conifer forests tend to have a dense understory composed of vascular plants that provides sufficient stalking cover (Macdonald and Fenniak 2007). Deer are the most common prey of cougars in my study area and commonly feed in open grassy areas (Knopff et al. 2010). Forests adjacent to open areas likely provides good stalking cover, and this edge habitat probably provides cougars with optimal hunting opportunity year around (Holmes and Laundré 2006).

Overall, cougars of all reproductive statuses and in both seasons had positive selection for areas closer to water, although not significant for females with kittens in winter. During the summer, areas closer to water were consistently among the most important habitat features for all groups of cougars. Similar results were reported by Dickson and Beier (2002) where cougars in southern California selected areas closer to riparian areas for both wet and dry seasons. Riparian habitat and areas closer to water are typically composed of dense cover and probably provide cougars in west-central Alberta with quality areas to stalk prey. In northern and southern

California, cougar kill sites were primarily located in creek bottoms and vegetation types associated with close proximity to water (Hopkins 1989, Beier et al. 1995).

Severe winter conditions decrease deer survival, resulting in lower densities in the late winter and spring (Delgiudice et al. 2002). The inclement weather conditions of Alberta winters can result in low prey availability and cougars may alter their hunting patterns to focus on more available prey during the spring and early summer. The thawing of streams and other water bodies in March and April allows beavers to become active on land, leaving the protection of their lodge (Bromley and Hood 2013). Cougars may travel along riparian and wetland areas in search of beavers during the early spring and summer months, amplifying their selection for this habitat type during the summer and frequent use of these areas was reflected in the telemetry data. Spring kill site investigations (n = 16) support this as 44% of female cougar kills were beaver, however no kill sites were investigated for male cougars (Smereka unpubl. data). Similar findings occurred in Washington where cougars commonly preyed upon beavers and deer along streams, rivers, wetlands and lakes (Kertson and Marzluff 2011). Cougars also had similar selection patterns for WL landcover type which was more important for habitat selection during the summer compared to winter for all groups and similar interpretations can be used for use of this habitat type.

Although insignificant for females with kittens in summer, our predictions for selection of forested over non-forested habitat were supported in that all groups selected the forested habitat type and were highly ranked for females with kittens in winter, males in winter and single females during both seasons. Structurally complex habitat, where individuals can remain concealed and prey do not aggregate in large groups, is commonly associated with solitary carnivores (Lamprecht 1978, Logan and Sweanor 2009). Cougars in North America evolved alongside wolves and bears, and selection for forested habitat may also be an adaptation to reduce the risk of scavenging or death by these competitors (Ruth and Murphy 2010). Where competing carnivores are absent, cougars may use open habitat more frequently, but still hunt in terrain that provides stalking cover (Elbroch and Wittmer 2012). In my study, cougars are the subordinate carnivore to bears and wolves, and evidence of both have been observed at cougar kill sites. I therefore suggest that forested habitat not only provides good hunting opportunity but also escape from bears and wolves for cougars of all sex and reproductive status as they often climb trees to avoid direct conflict with potential predators.

All cougars selected terrain that was steeper compared to what was available and is similar to other studies (Logan and Irwin 1985, Arundel et al. 2003, Kusler et al. 2017). White-tailed deer and mule deer tend to select sloped terrain (Pauley et al. 1993, Armleder et al. 1994) and Logan and Irwin (1985) suggest that cougar selection for such terrain may reflect use by deer, good stalking cover, and prey caching areas. Furthermore, cougars may use steeper terrain to avert interactions with dominant carnivores as well as provide thermoregulatory benefits during the winter (Kusler et al. 2017). Steep embankments along major rivers and sloped terrain in the west and southwest portion of the study area likely provide similar benefits to cougars.

Of the anthropogenic features in the top model, RD170 was the most important for cougar habitat selection except for females with kittens in summer. All groups avoided close proximity to roads, although for females with kittens, selection was not significant. My results supported the prediction that cougars of all reproductive statuses would avoid roads in both seasons and similar to past studies (Arundel et al. 2003, Knopff et al. 2014a), but see Dickson and Beier (2002) where cougars in southern California did not avoid roads once a home range was established. The southern California study had a high road density and non-avoidance of roads may be attributed to habituation to such areas. Roads however, can have many ecological effects on biotic communities including noise pollution (Spellerberg 1998). The eastern portion of my study area is highly fragmented due to resource extraction procedures and contains a dense network of logging and oilfield roads. The high frequency of large traffic such as oil tankers and logging trucks probably causes greater disturbance to wildlife in comparison to smaller traffic. Cougars are a cryptic species that live private lives and must rely on their own senses to detect prey and potential predators (Murphy and Ruth 2009). Noise pollution that occurs along roadways has been shown to affect an animal's ability to receive acoustic signals (Brumm 2004, Scobie et al. 2014). Similarly, if noise pollution or human disturbance is too great, it may prevent cougars from accurately detecting their surroundings and deterring them from roads. However, Knopff et al (2014) reported that cougars used areas closer to roads at night compared to day, and suggested that this could be due to deer using areas closer to roads to forage when vehicle activity is low.

Habitat selection was variable between season for all groups with some covariates being more important for selection during the summer than winter, and others more important during winter than summer. However, for males and especially single females the ranking of variables remained relatively consistent for both seasons. The seasonal differences are likely due to the abrupt environmental change brought about by winter and its effect on the availability of resources. Individual variation was the greatest for females with kittens in both seasons as indicated by the large IVW confidence intervals (Figure 3.2) and may indicate high behavioral differences of females with offspring. Furthermore, as kittens become older they require less parental care and by 4 months old are weaned and capable of climbing trees to escape predators (Logan and Sweanor 2009). Age of kittens may influence the choices females make with regards to habitat selection and could have resulted in the wide range of selection for KS and KW across most habitat variables. Separating females with kittens into two groups; those with highly dependent offspring and those with older offspring, may have allowed us to detect habitat selection differences but would have resulted in a much lower sample size. Because kittens are dependent on their mother until dispersal and the female's behavior likely reflects her need to provide for her offspring, I believed it to be appropriate to group females with young and old kittens together.

Overall, the mapped population level IVW obtained from the two-stage RSF, indicates that the highest relative habitat selection for all reproductive statuses occurs in the western portion of the study area and is especially true for females with and without kittens in the winter (Figure 3.3). The eastern portion of the study area is largely made up of agricultural lands with few large stands of forested habitat. Deep snow that accumulates in open habitat is probably energetically demanding to travel through and may make pursuit of prey or escape from predators more difficult (Crête and Larivière 2003). Furthermore, the use of forested landscapes, which are common and become less fragmented further west, likely provides thermoregulatory advantages for females with kittens, as they provide shelter from cold winter winds (Parker and Gillingham 1990). During the summer, relative habitat selection was more homogenous for all groups, indicating that the eastern region of the study area may provide suitable habitat for cougars.

The knowledge gained on habitat selection by cougars in west-central Alberta, Canada can be incorporated into cougar management planning by providing valuable information on where high quality habitat occurs, and if necessary, be used to implement harvest changes to mitigate human-cougar conflict while maintaining a viable population. Overall, cougars consistently selected for edge habitat, close proximity to water and forested areas, while avoiding close proximity to roads. Seasonally, habitat features appear to vary in importance for cougars of different sex and reproductive status, and is most evident for females with kittens. My results provide future studies on cougar and other carnivore ecology at northern latitudes with information on variables that are important for habitat selection.

Figures

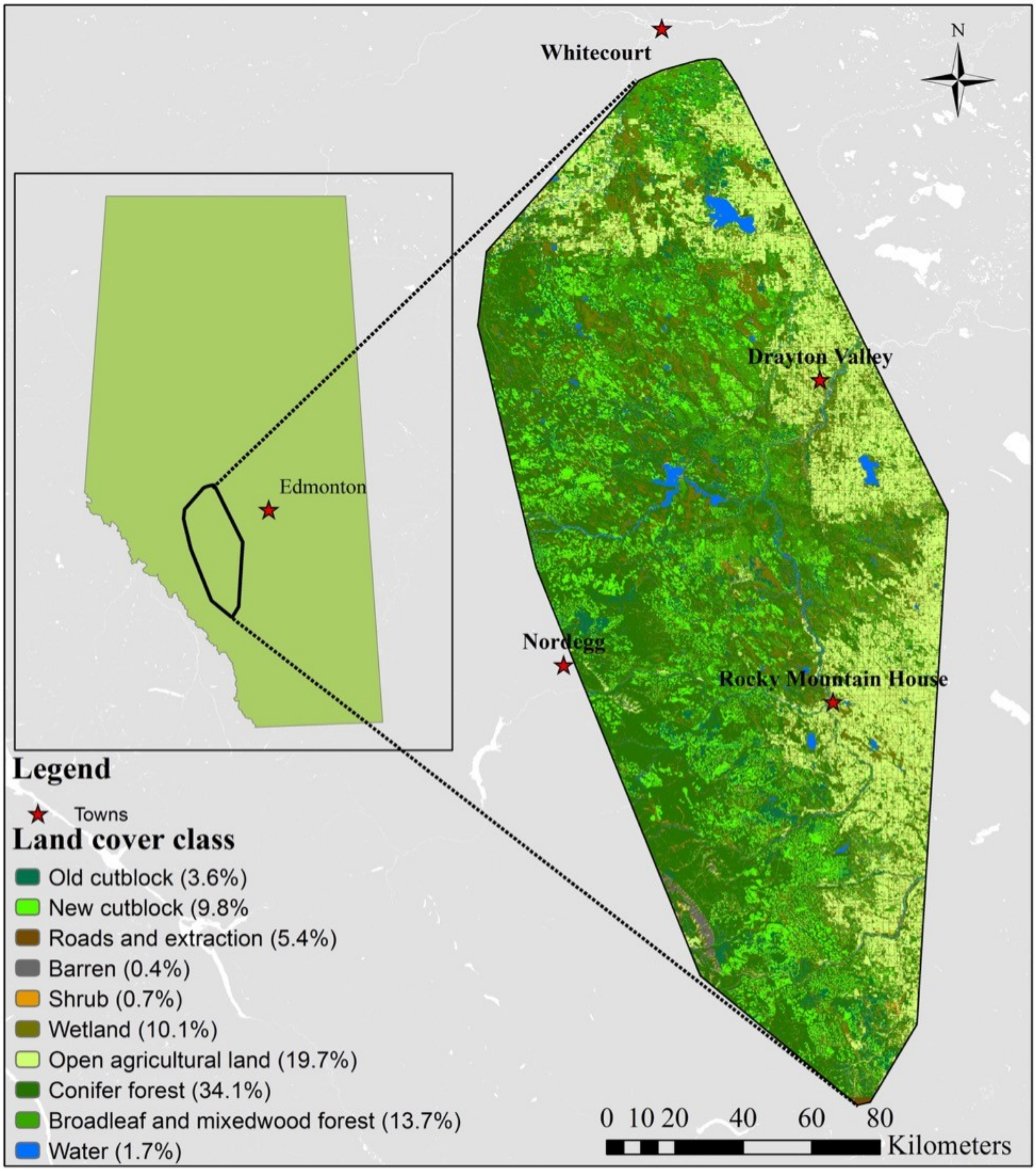

Whitecourt
N
Edmonton
Drayton Valley
Nordegg
Rocky Mountain House
Legend
Towns
Land cover class
Old cutblock (3.6%)
New cutblock (9.8%
Roads and extraction (5.4%)
Barren (0.4%)
Shrub (0.7%)
Wetland (10.1%)
Open agricultural land (19.7%)
Conifer forest (34.1%)
Broadleaf and mixedwood forest (13.7%)
Water (1.7%)
0 10 20 40 60 80
Kilometers

Figure 3.1 Study area location with *inset* showing the 100% minimum convex polygon where cougars were tracked from 2016-2018 in west-central Alberta, Canada. Legend indicates the landcover type and the proportion that made up the study area.

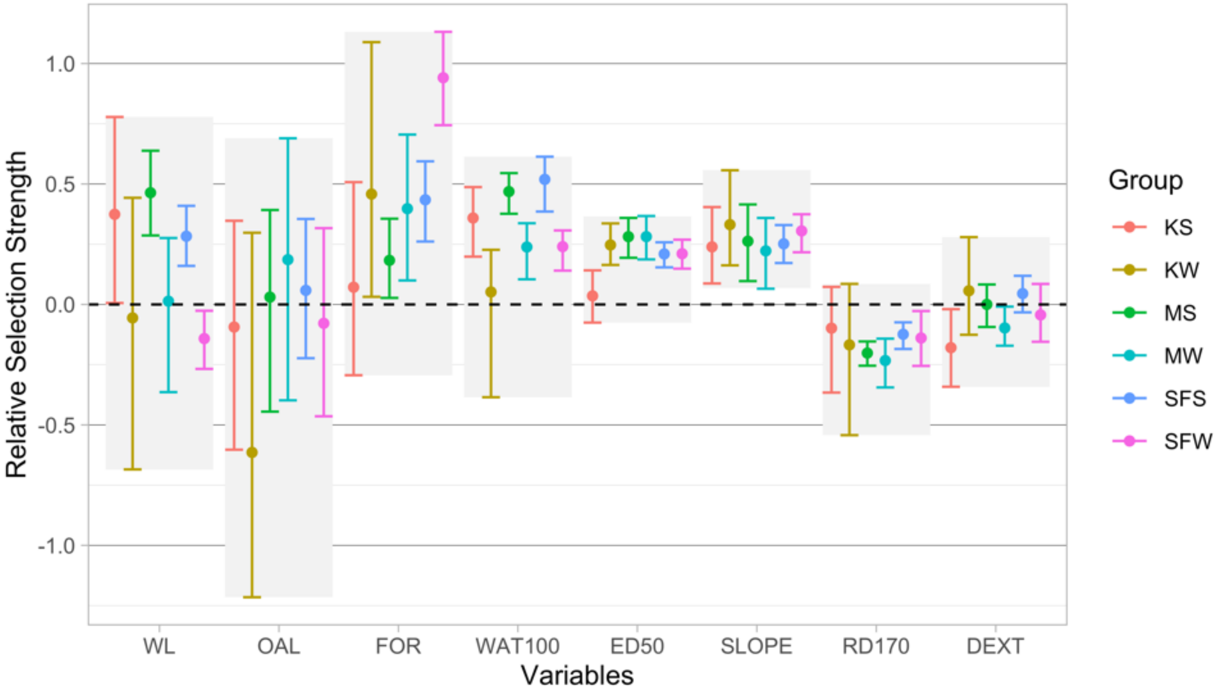
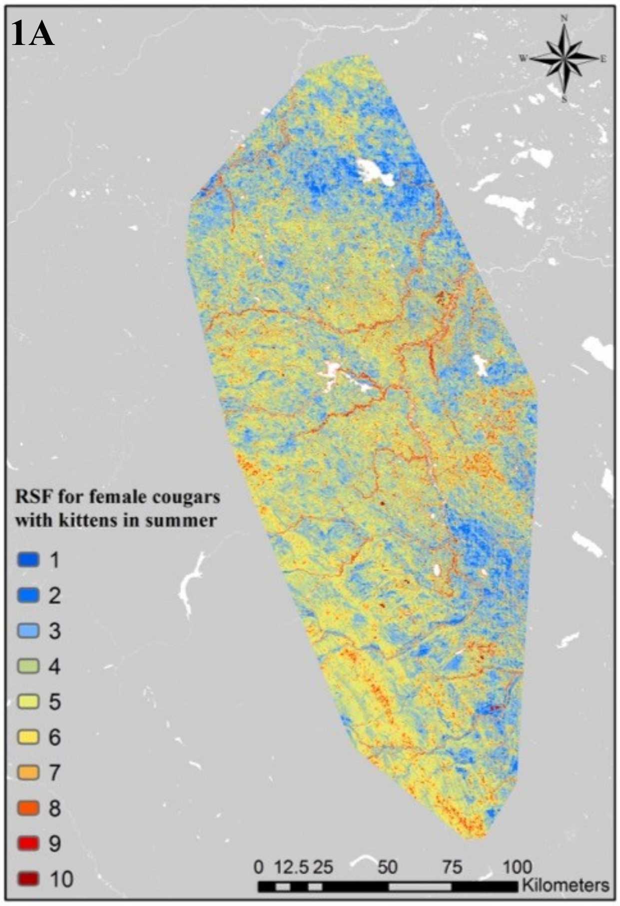


Figure 3.2 Relative selection strength for 8 landscape features from the combined model with 95% confidence intervals for female cougars with kittens in summer (KS), female cougars with kittens in winter (KW), adult male cougars in summer (MS), adult male cougars in winter (MW), single female cougars in summer (SFS), and single female cougars in winter (SFW). Beta coefficients and confidence intervals were calculated using inverse variance weighted mean (IVW) from the two-stage resource selection function after bootstrapping 4000 times.

1A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RSF for female cougars with kittens in summer
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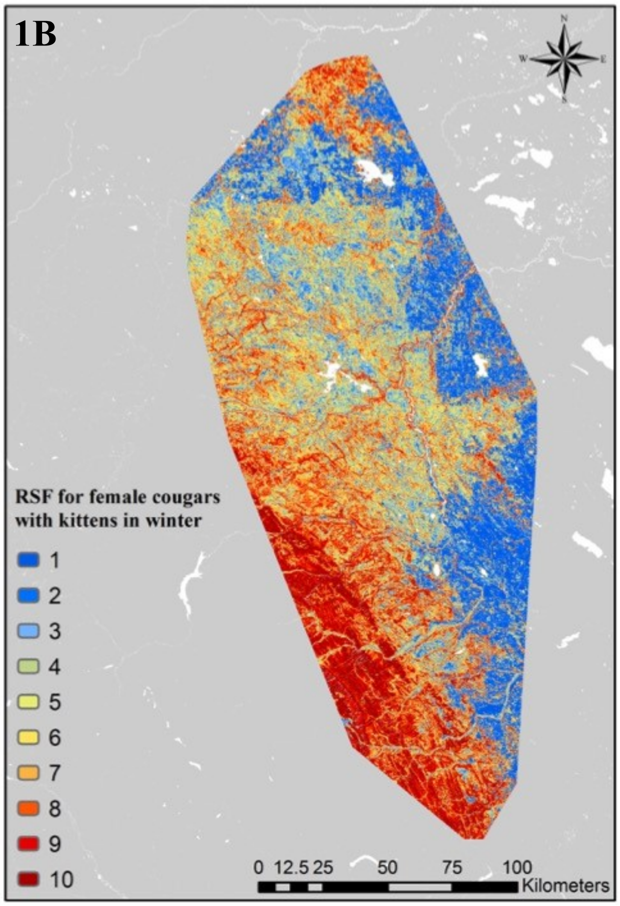
Kilometers

1B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RSF for female cougars with kittens in winter
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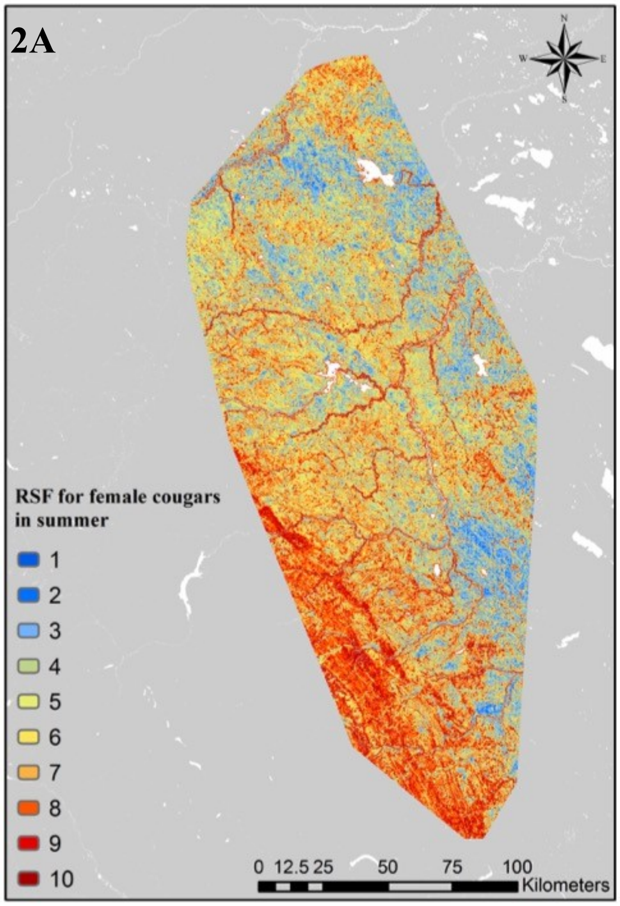
Kilometers

2A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RSF for female cougars in summer
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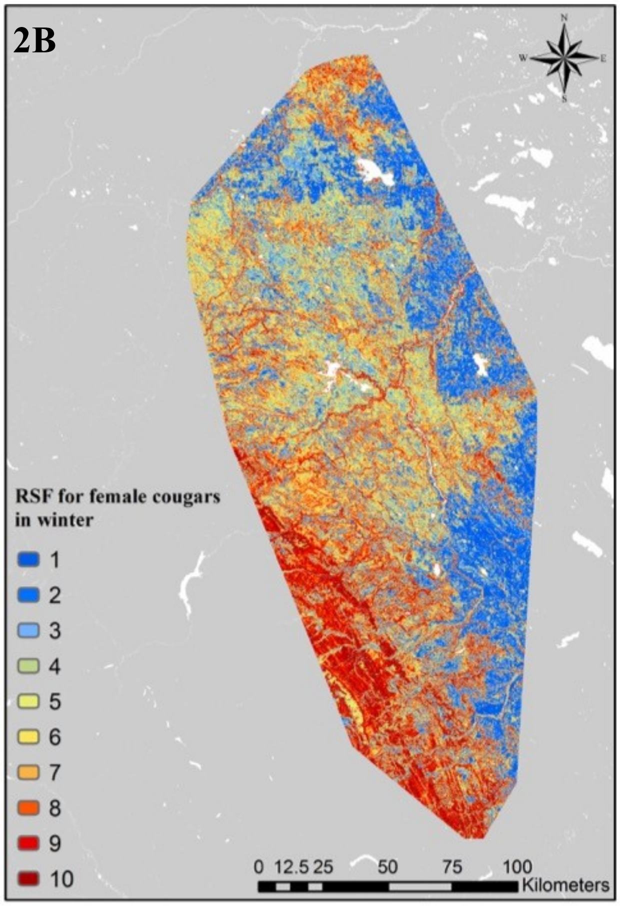
Kilometers

2B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RSF for female cougars in winter
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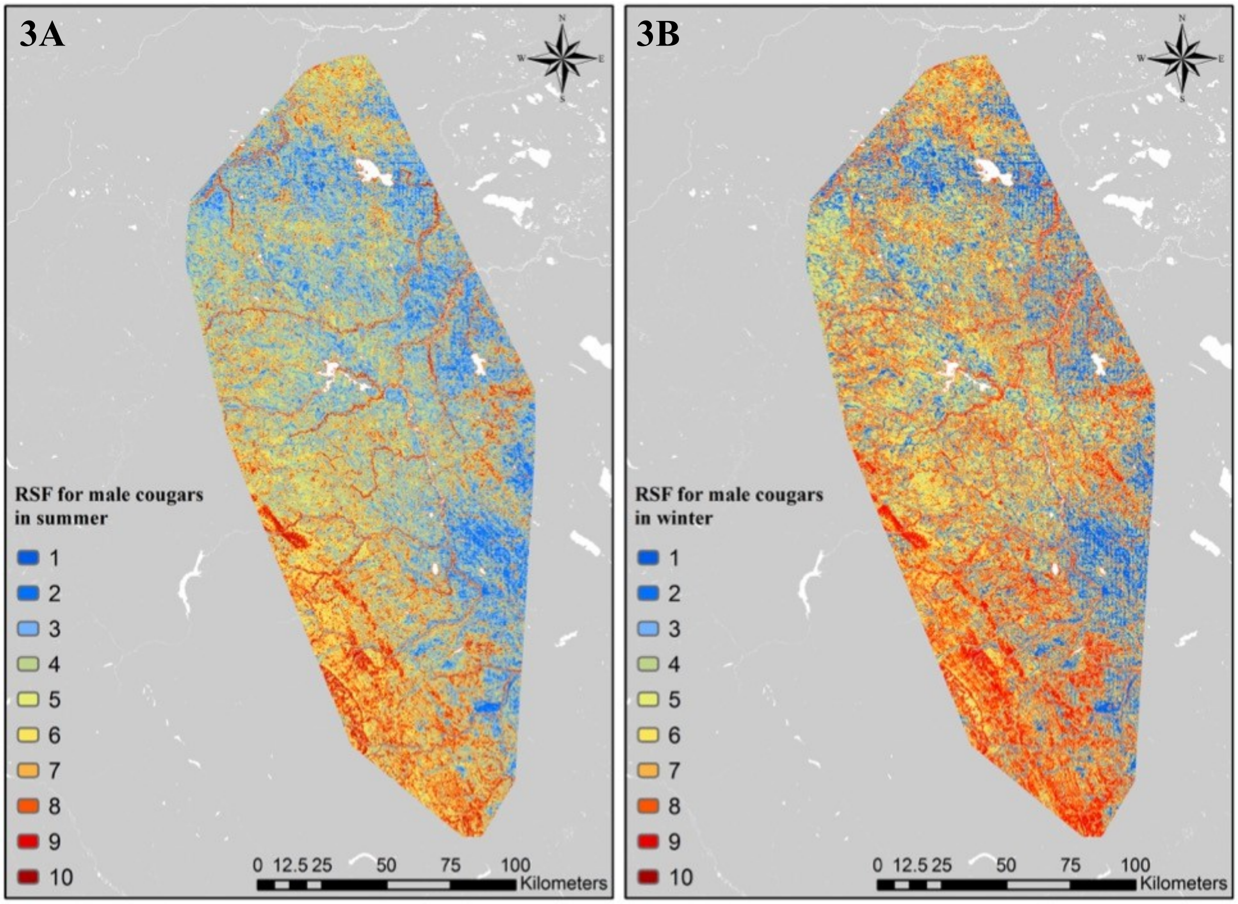

Figure 3.3 Maps showing the relative selection for female cougars with kittens in summer (1A) and winter (1B), single adult female cougars in summer (2A) and winter (2B), and adult male cougars in summer (3A) and winter (3B) in west-central Alberta, Canada. Blue areas indicate regions of low relative selection and orange to red areas high relative selection.

Table 3.1 Categorical and continuous landscape variables that were considered relevant to cougar habitat selection in west-central Alberta, Canada. The distance-to or exponential decay layer of the same class (i.e., Distance to road, Exponential decay of road (170m)) that had the best model fit based on AICc was used in model selection and is indicated with *.

Variable type	Class	Abbreviation	Type
Landcover			
	Old cutblock	OC	Binary
	New cutblock	NC	Binary
	Roads and Extraction	RE	Binary
	Barren	BN	Binary
	Shrub	SB	Binary
	Shrub and treed wetland	WL	Binary
	Open agricultural land	OAL	Binary
	Conifer forest	CF	Binary
	Broadleaf and mixedwood forest	BMF	Binary
	Water	WAT	Binary
	Forest (all forest landcover types)	FOR	Binary
Natural habitat			
	Distance to edge habitat	DEDGE	Continuous
	Exponential decay of edge habitat (30m)	ED30	Continuous
	Exponential decay of edge habitat (50m)*	ED50	Continuous
	Exponential decay of edge habitat (100m)	ED100	Continuous
	Distance to water (riparian or stagnant)	DWAT	Continuous
	Exponential decay of water habitat (30m)	WAT30	Continuous
	Exponential decay of water habitat (50m)	WAT50	Continuous
	Exponential decay of water habitat (100m)*	WAT100	Continuous
	Slope of terrain	SLOPE	Continuous
	Digital elevation model (DEM)	ELEV	Continuous
	Terrain ruggedness index (TRI)	TRI	Continuous
Prey			
	Deer use/availability layer	DEER	Continuous
	Moose use/availability layer	MOOSE	Continuous
Anthropogenic			
	Distance to road	DROAD	Continuous
	Exponential decay of road (170m)*	RD170	Continuous
	Distance to resource extraction	DEXT	Continuous
	Distance to residential areas	DRES	Continuous
	Exponential decay of residential areas (210m)*	RES210	Continuous

Table 3.2 Candidate RSF models

Model	No. of Covariates	Model Structure
Prey	3	DEER + DEER^2 + LN_MOOSE
PreyHabitat	4	DEER + DEER^2 + WAT100 + ED50
Habitat	9	OC + NC + RE + WL + OAL + BMF + WAT100 + LN_TRI + LN_ELEV
Anthropogenic	7	LN_DEXT + RE + OAL + NC + RES210 + RD170 + FOR
Safety	6	LN_SLOPE + WL + CF + BMF + RD170 + LN_DEXT
Combined	8	LN_SLOPE + WL + OAL + RD170 + LN_DEXT + WAT100 + ED50 + FOR

Table 3.3 Seasonally stratified population level coefficients (IVW) for males in summer and winter in west-central, Alberta, Canada. The contribution of each variable to the model is indicated by the rank column.

	MS				***MW***			
Variables	**IVW**	**rank**	**LCI**	**UCI**	**IVW**	**rank**	**LCI**	**UCI**
WL	0.464	2	0.287	0.638	0.014	8	-0.364	0.276
OAL	0.030	7	-0.445	0.392	0.186	6	-0.398	0.690
FOR	0.183	6	0.027	0.356	0.398	1	0.100	0.705
WAT100	0.469	1	0.376	0.545	0.239	3	0.104	0.337
ED50	0.281	3	0.194	0.359	0.282	2	0.187	0.367
SLOPE	0.263	4	0.097	0.415	0.222	5	0.065	0.359
RD170	-0.202	5	-0.254	-0.154	-0.233	4	-0.345	-0.142
DEXT	0.000	8	-0.093	0.083	-0.098	7	-0.171	-0.009

Table 3.4 Seasonally stratified population level coefficients (IVW) for single females in summer and winter in west-central, Alberta, Canada. The contribution of each variable to the model is indicated by the rank column.

	SFS				***SFW***			
Variables	**IVW**	**rank**	**LCI**	**UCI**	**IVW**	**rank**	**LCI**	**UCI**
WL	0.283	3	0.160	0.409	-0.142	5	-0.268	-0.026
OAL	0.058	7	-0.223	0.355	-0.078	7	-0.464	0.317
FOR	0.434	2	0.261	0.594	0.941	1	0.744	1.132
WAT100	0.519	1	0.386	0.613	0.240	3	0.140	0.307
ED50	0.210	5	0.154	0.258	0.211	4	0.149	0.269
SLOPE	0.252	4	0.172	0.329	0.305	2	0.217	0.374
RD170	-0.124	6	-0.185	-0.074	-0.139	6	-0.255	-0.027
DEXT	0.045	8	-0.033	0.119	-0.043	8	-0.155	0.085

Table 3.5 Seasonally stratified population level coefficients (IVW) for females with kittens in summer and winter in west-central, Alberta, Canada. The contribution of each variable to the model is indicated by the rank column.

	KS				***KW***			
Variables	**IVW**	**rank**	**LCI**	**UCI**	**IVW**	**rank**	**LCI**	**UCI**
WL	0.374	1	0.006	0.778	-0.056	7	-0.685	0.443
OAL	-0.094	6	-0.603	0.347	-0.614	1	-1.215	0.298
FOR	0.071	7	-0.294	0.508	0.458	2	0.032	1.089
WAT100	0.359	2	0.198	0.487	0.052	8	-0.385	0.227
ED50	0.036	8	-0.075	0.142	0.247	4	0.164	0.336
SLOPE	0.239	3	0.087	0.404	0.331	3	0.162	0.557
RD170	-0.099	5	-0.366	0.073	-0.168	5	-0.543	0.085
DEXT	-0.179	4	-0.342	-0.020	0.057	6	-0.126	0.279

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3.6 Appendix

Table A3.1 Table comparing selection coefficients from mixed effects RSF (ME) and the inverse variance weighted means from two-step RSF with 4000 bootstrap iterations (IVW). P-value < 0.05 indicated by *.

Variable	**MW**		**MS**		**SFW**		**SFS**		**KW**		**KS**	
	IVW	**ME**	**IVW**	**ME**	**IVW**	**ME**	**IVW**	**ME**	**IVW**	**ME**	**IVW**	**ME**
WL	-0.01	-0.06	0.46*	0.49*	-0.14*	-0.18*	0.28*	0.27*	0.06	-0.34	0.37*	0.34*
OAL	0.19	0.09	0.03	-0.04	-0.08	-0.30*	0.06	-0.17*	-0.61	-1.16	-0.09	-0.46*
FOR	0.40*	0.46*	0.18*	0.22*	0.94*	0.98*	0.43*	0.47*	0.46*	0.55*	0.07	0.15*
WAT100	0.24*	0.21*	0.47*	0.47*	0.21*	0.25*	0.52*	0.55*	0.05*	-0.14*	0.36*	0.31*
ED50	0.28*	0.27*	0.28*	0.28*	0.21*	0.21*	0.21*	0.21*	0.25*	0.24*	0.04	0.04*
LN_SLOPE	0.22*	0.22*	0.26*	0.28*	0.31*	0.30*	0.25*	0.26*	0.33*	0.44*	0.24	0.25*
RD170	-0.23*	-0.26*	-0.20	-0.22	-0.14*	-0.17*	-0.12*	-0.16*	-0.17	-0.30*	-0.1	-0.15*
LN_DEXT	-0.10*	-0.07*	<0.01	0.01	-0.04	<0.01	-0.05	0.07	0.06	0.14*	-0.18*	-0.13*

Table A3.2 Table indicating model weights for KS

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Combined	10	24040.48	0.00	1.00	1.00	-12010.24
Anthropogenic	9	24057.60	17.13	0.00	1.00	-12019.80
PreyHabitat	6	24066.19	25.72	0.00	1.00	-12027.10
Safety	8	24133.88	93.40	0.00	1.00	-12058.94
Prey	5	24172.26	131.78	0.00	1.00	-12081.13
Habitat	11	24190.49	150.01	0.00	1.00	-12084.24
Null	2	24568.91	528.43	0.00	1.00	-12282.46

Table A3.3 Table indicating model weights for KW

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Combined	10	20951.31	0.00	1.00	1.00	-10465.65
Safety	8	21175.08	223.78	0.00	1.00	-10579.54
Habitat	11	21440.21	488.90	0.00	1.00	-10709.10
Anthropogenic	9	21529.20	577.89	0.00	1.00	-10755.60
PreyHabitat	6	21959.51	1008.20	0.00	1.00	-10973.75
Prey	5	22000.91	1049.60	0.00	1.00	-10995.45
Null	2	22408.45	1457.14	0.00	1.00	-11202.22

Table A3.4 Table indicating model weights for MS

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Combined	10	54133.44	0.00	1.00	1.00	-27056.72
Habitat	11	55150.88	1017.44	0.00	1.00	-27564.44
PreyHabitat	6	55258.05	1124.62	0.00	1.00	-27623.03
Safety	8	55733.05	1599.61	0.00	1.00	-27858.52
Anthropogenic	9	56547.48	2414.05	0.00	1.00	-28264.74
Prey	5	56959.23	2825.80	0.00	1.00	-28474.62
Null	2	57066.46	2933.02	0.00	1.00	-28531.23

Table A3.5 Table indicating model weights for MW

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Combined	10	35321.15	0.00	1.00	1.00	-17650.57
Safety	8	35617.06	295.91	0.00	1.00	-17800.53
PreyHabitat	6	35684.60	363.45	0.00	1.00	-17836.30
Habitat	11	35793.98	472.84	0.00	1.00	-17885.99
Anthropogenic	9	35878.95	557.81	0.00	1.00	-17930.48
Prey	5	35999.33	678.19	0.00	1.00	-17994.66
Null	2	36187.10	865.95	0.00	1.00	-18091.55

Table A3.6 Table indicating model weights for SFS

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Combined	10	105911.0	0.00	1.00	1.00	-52945.52
PreyHabitat	11	107415.1	1504.03	0.00	1.00	-53696.54
Prey	6	108541.1	2630.05	0.00	1.00	-54264.54
Safety	8	109774.5	3863.48	0.00	1.00	-54879.26
Anthropogenic	9	111253.9	5342.81	0.00	1.00	-55617.93
Prey	5	112727.6	6816.53	0.00	1.00	-56358.78
Null	2	113098.8	7187.75	0.00	1.00	-56547.39

Table A3.7 Table indicating model weights for SFW

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	LL
Combined	10	70710.29	0.00	1.00	1.00	-35345.14
Safety	8	71236.67	526.38	0.00	1.00	-35610.33
Habitat	11	71756.87	1046.58	0.00	1.00	-35867.44
Anthropogenic	9	72434.05	1723.76	0.00	1.00	-36208.03
PreyHabitat	6	72439.04	1728.75	0.00	1.00	-36213.52
Prey	5	73062.11	2351.82	0.00	1.00	-36526.06
Null	2	74253.60	3543.31	0.00	1.00	-37124.80

Chapter 4

4.1 Conclusion

One of the greatest issues facing wildlife managers and conservation biologists globally is dealing with human-wildlife conflict (Dickman 2010). Conflict is diverse and can range from small rodents or large herbivores raiding crops (Layne 1997, Perez and Pacheco 2006), depredation of livestock (Kaczensky 1999, Muhly and Musiani 2009), disease transmission to humans (Taylor et al. 2001, Wolfe et al. 2005), and direct attacks on people (Loe and Roskaft 2004). Large felids occur in most regions of the world and conflict with people is common (Beier 1991, Saberwal et al. 1994, Bagchi and Mishra 2006, Michalski et al. 2006, Barlow 2009, Inskip and Zimmermann 2009). Mitigating conflict between large felids and people tends to be in the form of direct removal through harvest (Strickland et al. 1994). However, if the geographic scale of harvest and the response of the species is not carefully considered, the result may be unintended population decline (Reynolds and Tapper 1996, Frank and Woodroffe 2001).

With regards to cougar conservation, the single biggest obstacle to overcome is dealing with human-cougar conflict (Hornocker and Negri 2009). Human populations in North America are projected to increase over the next century and with it, the likelihood of increased human-cougar conflict (Hornocker and Negri 2009). More conflict will undoubtedly call for increased persecution of cougars, especially from people living in rural areas where interactions are more likely to occur. Therefore, the challenge becomes balancing an acceptable level of human-cougar conflict while maintaining viable cougar populations. To decrease conflict, managers may implement increased harvest quotas or modify harvest regulations. However, increasing harvest may affect the social structure of cougar populations resulting in unintended consequences (Hornocker 1969, Maletzke 2010, Beausoleil et al. 2013).

A stable cougar population is defined as a population that is made up of mature females, females with offspring, dispersing individuals, and mature males which maintain stability through rigorous territorial behavior, preventing young individuals from establishing a home range (Hornocker and Negri 2009). The demographic most responsible for conflict with people are young individuals that have recently been deserted by their mother and are inexperienced in hunting (Beier 1991). Increased harvest of mature males may create habitat vacancies where younger individuals can establish a home range. Therefore, increasing harvest may increase human-cougar conflict if harvest is focused on mature males. Although adult male cougars are hunted in Alberta, targeting younger individuals may be the best way to reduce conflict with people. Understanding whether a population has a stable social structure can be a challenge within itself, making it difficult to implement appropriate harvest regulations. Therefore, I suggest that the first step in managing cougar populations for both population viability and reduction in human-cougar conflict is to assess social structure of a population. Gaining knowledge on social structure may be accomplished by determining the different space use patterns that occur and their proportion in a population, with more dynamic patterns possibly reflecting a more unstable population. To understand social structure, I first recommend a manipulative study where comparison of home range dynamics, such as space use patterns, can be made in areas with high human-caused harvest and little to no human-caused harvest. Second, I recommend investigating if increased cougar mortality significantly lowers genetic diversity of the population.

Maintaining a viable population relies on recruitment into the population, hence overharvesting subadults could be detrimental to the population. To balance a healthy cougar population with low human conflict, source and sink areas should be recognized and this may be accomplished with the help of resource selection functions (RSFs) (Boyce and McDonald 1999). RSFs can help identify high quality habitat which could indicate regions where conflict is likely to be high, but also areas where cougars may occur with little human interaction. In my study area, Cougar Management Areas 11 and 21 contain large portions of fringe habitat to the east where human density is high but forested areas adjoining agricultural lands provides quality habitat for cougars. The close proximity to people is likely to increase confrontations. It may be appropriate to treat these regions and similar areas across Alberta as sink populations, where harvest is liberal, especially for young, inexperienced cougars that are more likely to get into conflict with people. The western portion of the study area, has much lower densities of people but provide the highest quality cougar habitat and could be managed as source populations. Lower overall harvest should maintain a stable social structure in the source population. Emigrating individuals, especially males, may repopulate surrounding areas where there is higher harvest and infill vacancies left by individuals that have died by natural cause or in low harvest areas.

Cougars are a cryptic species that generally live in low densities which makes population and density estimates one of the most challenging questions with regards to cougar research and management. Genetic analysis is an important tool for population monitoring and can help in estimating population connectivity, which is especially important for cougar populations living on fragmented landscapes (Jenks 2011). Additionally, genetic data can help estimate population size and detect the occurrence of a genetic bottleneck or severe inbreeding (Jenks 2011), both of which can cause extirpation of a species and should be considered by wildlife managers. Genetic data compounded with information on home range dynamics (i.e., size, overlap, space use pattern) can help in determining the population size of cougars in a given area. Information on habitat quality, population size and stability, genetics, past harvest and occurrences of human-cougar conflict can be incorporated into an adaptive management framework where management goals can be achieved by continually modifying management prescriptions such as harvest.

With respect to my work in Chapters 2 and 3, improvements may have been made by 1) applying cougar harvest data to determine if space use patterns, such as seasonal shifter or shifter occurred after removal of a neighboring individual, 2) acquiring more prey data to increase the robustness of the deer and moose use versus availability layers, 3) using higher resolution and more recent land cover data in my RSF, 4) incorporating understory vegetation data to better predict suitable stalking cover, and 5) increase specificity in the timing of female cougar offspring care.

The projected human population growth of the 21st century is likely to cause an increase in human-cougar conflict, and although cougar research has increased since the 1970s, more information needs to be gathered if wildlife managers are going to successfully conserve a species that is already prone to conflict with people. If we are to achieve coexistence with this large carnivore, some future research recommendations are to: 1) determine the effect age or sex specific harvest, especially that of mature adult males, has on population social structure and human-cougar conflict, 2) investigate the space use response of cougars after neighboring individuals have been removed, 3) prolong space use monitoring to determine dynamics over multiple years, 4) investigate what causes different space use patterns of adults (i.e., prey availability, density, harvest), 5) assess home range overlap between and among sexes in high and low harvest populations, 6) measure relatedness of overlapping individuals and whether matrilineal assemblages occur, 7) assess female and kitten survival in high harvest populations where infanticide may be increased due to high male turnover, 8) examine if human exploitation of large mature males, which are typically favored by females for breeding, relaxes sexual selection, 9) use habitat suitability maps to help establish areas where source and sink populations can be managed appropriately to sustain a healthy population and reduce human-cougar conflict, 10) use genetic analysis to help understand source and sink dynamics of a region and how related individuals interact with each other, 11) generate population and density estimates while incorporating information on home range dynamics, and 12) model how climate change will affect cougar distributions across their geographic range. Answering these questions will help to aid management of cougars so that populations can fulfil their ecological role on the landscape.

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