Biological and environmental correlates of cougar (*Puma concolor*) survival in west central Alberta

by

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Abstract

Large carnivores have a significant role in ecosystems and their role as apex predators can have cascading effects that influence ecosystem stability. Managing large carnivores requires an understanding of how they use the land and their vital rates, including survival. For cougars (*Puma concolor*), habitat selection is well documented, but the hazards that cougars face across the landscape are poorly understood. The risks that landscape features present can change temporally, increasing survival in one season while being a danger in another. Between 2016 – 2021 87 cougars were radio-collared and tracked in west central Alberta, Canada, for a total of 1158 cougar months with a mean monitoring time of 13.3 months. I documented 41 deaths, determined causes of mortality, generated survival estimates using Kaplan-Meier models by sex and age class annually and for each season [i.e., summer, winter, and hunting (a subset of winter)], and investigated hazards using Cox proportional hazard models. Humans were responsible for 33 of the 41 mortalities reported, with legal harvest being the highest cause of mortality (16/41 mortalities) for both males and females, with males more likely to be harvested. However, I was unable to detect a difference in survival estimates between sexes or age classes. Annual male subadult survival was 0.857 (CI = 0.633 - 1), male adult survival was 0.586 (CI = 0.406 - 0.845), female subadult survival was 0.857 (CI = 0.629 – 1) and female adult survival was 0.628 (CI = 0.512 – 0.770). While survival estimates of both sexes were lowest in the hunting season, I was unable to detect a difference in survival by season. I modelled the risk that biological and environmental variables imposed on each sex using Cox proportional hazards models with the Anderson-Gill model for staggered entry. Hazards differed by sex annually with both sexes showing increased hazard with high crossing rates of secondary roads and linear features, closer proximity to secondary roads and closer proximity and higher density of residential areas. Sexes differed with males showing increased hazard in open areas and wetlands and areas further from water. Females showed no difference in risk by landcover classification or distance to water but showed increased risk with higher primary road crossing rates. Hazards also varied between sexes within 2 of the seasons investigated. In the winter season both sexes had an increased risk with higher crossing rates of secondary roads and linear features as well as increasing proximity to secondary roads. Males also showed increased risk at higher residential densities and closer proximities. Females however had an increased risk with increased crossing rates of primary roads, and lower terrain ruggedness. Additionally, age class significantly influenced risk of males, with male kittens and subadults being higher risk than male adults, as well as increased risk within open areas and closer proximity to secondary roads. Females had increased risk with higher crossing rates of secondary roads and linear features and increased proximity and density of residences. Survival also was examined at a short temporal scale (ca. 48h) to determine proximate variables that resulted in death. For males 48hrs before death, I found kittens and subadults to be at higher risk than adults and that open areas, shrublands, and wetlands all increased risk as well as closer proximity to roads. For females, I found closer proximity to secondary roads and increasing residential density increased risk. Our results provide insight on how biological and environmental variables affect cougar survival and how hazards vary between sexes.

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1.1 Introduction

Large carnivores play important roles in the function and stability of ecosystems. Their role as apex predators affects both herbivore populations that may result in cascading affects that alter vegetation and avifauna, as well as mesocarnivore ecology through intraguild competition (Noss et al., 1996; Ritchie & Johnson, 2009; Ripple et al., 2014; Hebblewhite & Whittington, 2020). Within North America, land conversion, hunting, and directed persecution (e.g., bounties) reduced the abundance of large carnivores by the early twentieth century, since then, effort has been made to restore many of these populations (Miller et al., 2013; Teichman et al., 2016). Effectively managing large carnivores, and ensuring population viability, requires an understanding of carnivore population dynamics, and thus vital rates such as survival (Treves & Karanth, 2003; Clark et al., 2015).

Survival of large carnivores is affected by individual biological factors (e.g., age and sex) (Lee et al., 2005; Boulanger et al., 2013; Gardner et al., 2014; Keehner et al., 2015) as well as environmental factors (e.g., habitat type, prey, and weather) (Hebblewhite et al., 2003; Nielsen et al., 2004a; Hiller et al., 2015; Keehner et al., 2015). Predicting factors that influence survival and how they affect it can be challenging. In some instances, traits or areas that could confer higher survival instead have lower survival due to human-caused mortality (e.g., larger individuals being preferentially harvested), which in many large carnivores is greater than natural mortality (Benn & Herrero, 2002; Holmes & Laundré, 2006; Boulanger et al., 2013). Further, a single factor can have multiple, potentially conflicting effects on survival and can affect the overall survival differently between classes based on biological characteristics (Boulanger et al., 2013; Keehner et al., 2015; Smereka et al., 2021). Due to differences between sexes, the hazards that biological and environmental factors present should be examined for each sex separately.

Cougars (*Puma concolor*) are an apex predator with a wide distribution across North America and South America and their populations are often regulated through hunting (adjusting quotas) and other mortality from anthropogenic sources (e.g., conflicts) are often higher than natural factors (McKinney et al., 2009; Young et al., 2010; Schwab & Zandbergen, 2011; Wolfe et al., 2015). Natural sources of mortality include intraspecific aggression (McKinney et al., 2009), disease (Wolfe et al., 2015), infanticide (Logan & Sweanor, 2001), and predation from both conspecifics and other species (Ruth et al., 2011). While humans may be the main mortality factor, cougar survival rates are influenced by both biological factors and environmental variables (Young et al., 2010; Clark et al., 2015). Biological factors affecting survival of cougars include age, sex, offspring, and behavior (e.g., home range fidelity, linear feature crossing rate) (Knopff et al., 2014; Dickie et al., 2017; Smereka et al., 2020). Age can influence risk from harvest because older individuals are preferably harvested, but also through use of the environment (Cooley et al., 2009). Subadults and adults differ in their use of the environment with subadults leaving natal ranges and dispersing into new areas to establish home ranges away from adults and siblings (McLellan & Hovey, 2001; Morrison et al., 2015). During dispersal movements individuals can have increased mortality risk from multiple factors, whether its intraspecific competition or anthropogenic sources due to naïve behaviors in novel habitats (Thorsen et al., 2022). Resident adults with an established home range may also have differing levels of risk depending on their home range fidelity. Individuals with a higher home range fidelity may have higher survival due to spatial familiarity and increased efficiency acquiring prey within their home range (Smereka et al., 2021). Dependent offspring can influence survival of females through intraspecific conflict with potentially infanticidal males, or through risks involved with occupying lower quality habitats to avoid males (Keehner et al., 2015).

Environmental factors affecting cougar survival include weather, landcover types, topography, and anthropogenic activity (Smith et al., 2015; Dellinger et al., 2019). Habitat associations play a large role in cougar survival as they contribute to natural mortality rates through prey availability, nursery sites, and shelter quality and availability, as well as anthropogenic mortality (Knopff et al., 2014). Differing habitat types have unique risks, but are also used to fulfil a specific need, such as edge habitats for hunting and densely wooded areas for nursery sites (Holmes & Laundré, 2006; Benson et al., 2008; Elbroch et al., 2015). While studies have examined the role of environmental variables on cougar habitat selection, the influence of habitat on survival is poorly understood.

Environmental variables can influence cougar survival through natural causes such as prey availability, as well as through anthropogenic means, such as access by hunters or depredation kills (Ruth et al., 2011). The interactions between cougars and humans can result in complex relationships that affect survival. Anthropogenic areas may present a direct threat to cougars as many rural areas allow landowners are to kill them year-round. Further, anthropogenic areas can alter cougar energetic demands, reduce revisitation rates of cached food subsequently increasing kill rates that ultimately result in higher energy expenditure (Smith et al., 2015). Cougars show flexible behavior by adjusting activity times in response to anthropogenic development and use anthropogenic areas at less busy times (Knopff et al., 2014; Morrison et al., 2014). While cougars generally avoid anthropogenic areas with high human densities, this avoidance itself may reduce survival if cougars select for lower quality habitats to avoid humans (Kertson et al., 2011; Peebles et al., 2013; Dellinger et al., 2019).

A single variable can influence survival in different ways. For example, secondary roads may increase survival of all cougars through higher hunting efficiency but conversely may increase their vulnerability to harvest if their tracks are easier for hunters to find (Dellinger et al., 2019). The response to environmental variables also can differ between groups or classes based on biological characteristics. For example, secondary road use may increase hunting efficiency for both sexes, but because males are preferentially harvested, secondary road use may decrease their survival more than females if their tracks are encountered by hunters. Increased crossing of primary roads may also decrease survival of both sexes through vehicle collisions, however, females show a stronger "cage effect" (i.e., hesitancy to cross roads), therefore road density may affect males more than females (Schwab & Zandbergen, 2011; Banfield et al., 2020). Temporal variation also can influence whether a variable influences survival. While crossing secondary roads may lower survival during the hunting season, outside of this season without harvest risk, secondary roads use may increase survival by increasing hunting efficiency. Other variables affecting survival may remain the same year-round, for example, the risk of vehicle collisions. That a single variable can have multiple, potentially conflicting, effects on survival makes predicting whether a variable will increase or decrease survival challenging.

The objective of this study was to determine causes of mortality, estimate survival rates of cougars by age class and sex, and assess how biological and environmental variables influence mortality risk of each sex annually, seasonally, and at short temporal scales (ca. 48h) in west central Alberta, Canada. The short temporal scale investigates proximate variables that result in death (e.g., crossing roads with fresh snow). The study used satellite telemetry data collected on cougars from 2016 to 2021 using the location where known mortalities occurred to assess biological and environmental variables correlated with mortality.

Given that the region is managed for sport hunting, I hypothesized that: 1) male survival will be lower than females due to harvest, 2) harvest will be the primary cause of mortality for both sexes, 3) variables predicted to lower survival of all cougars annually include use of agriculture areas, industrial and residential sites, and close proximity to roads, 4) variables that increase harvest risk are expected to increase mortality of all cougars in the hunting season, with a greater increase for males compared to females and include higher crossing rates of roads and linear features, lower elevation, lower terrain ruggedness, lower slope, open areas, shrubland, fresh snow, and closer proximity to roads.

1.2 Methods

1.2.1 Study Area - The study area was in west central Alberta, Canada, south of Whitecourt, west of Rocky Mountain House, north of Sundre, and east of the Rocky Mountains (Fig. 1.1). Alberta manages cougar harvest using 32 cougar management areas (CMAs) and sex selective harvest quotas for each CMA (Government of Alberta, 2012). Cougars were collared within the Cougar Management Areas (CMAs) 11, 12, and 21 and I defined the study area as the 100% minimum convex polygon encompassing all collar points in R, which included additional CMAs that cougars dispersed into. The area transitions from mountainous terrain to prairies and agriculture land, and contains alpine, subalpine, upper and lower foothills, and mixed forest ecoregions (Downing & Pettapiece, 2006). Forested areas are comprised largely of white spruce (*Picea glauca*), black spruce (*P. mariana*), lodgepole pine (*Pinus contorta*), jack pine (*P. banksiana*), and tamarack (*Larix laricina*) with trembling aspen (*Populus tremuloides*) and balsam poplar (*P.*

balsamifera) in smaller patches (Downing & Pettapiece, 2006). The main prey in the area is white-tailed deer (*Odocoileus virginianus*) with other common ungulate and non-ungulate prey including mule deer (*O. hemionus*), moose (*Alces alces*), elk (*Cervus elaphus*) and beaver (*Castor canadensis*) (Knopff et al., 2010a). Other large carnivores present include wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*U. arctos*). Logging and oil and gas activity is common throughout the landscape and have resulted in extensive secondary road networks.

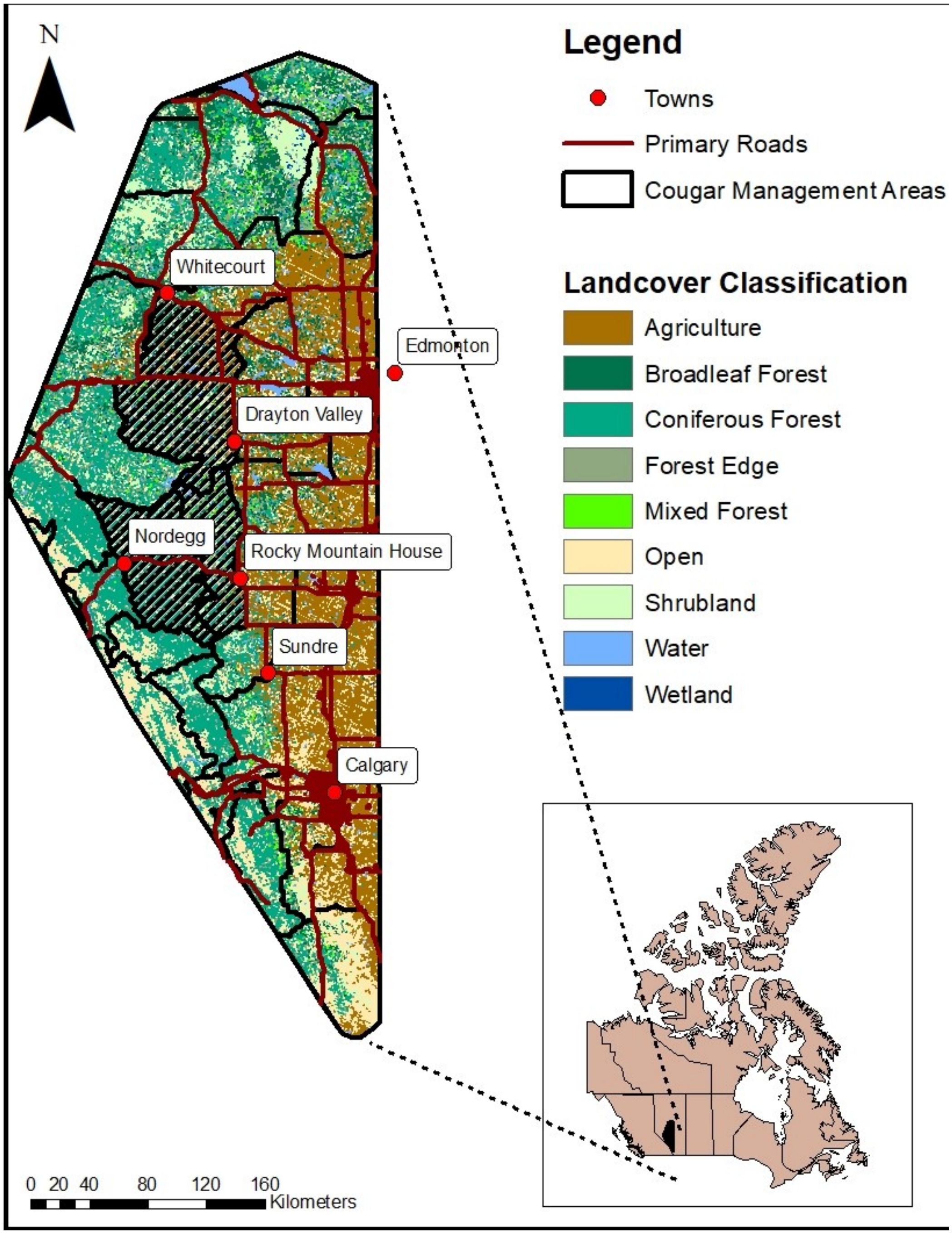

Figure 1.1. Study area in west central Alberta showing the cougar management areas, hatched areas represent CMAs where collars were deployed. Insert shows the study area designated as the 100% minimum convex polygon encompassing all collar points.

1.2.2 Capture, Handling, and Telemetry Data – Cougars were located by searching roads for tracks and hounds were used to trail and tree cougars, which were then immobilized using a Dan-inject CO2 rifle (Dan-Inject, Kolding, Denmark) and darts containing medetomidine (0.05-0.075 mg/kg) and Telazol (1.7-2.6 mg/kg) (MZT) (Smereka et al., 2021). MZT was reversed following handling using atipamezole (0.4 mg/kg). Immobilized animals were removed from trees, weighed, sexed, aged using gum-line recession, tooth wear and color and spotting of pelage (McKinney et al., 2009), and fitted with a geographic positioning system (GPS) collar (Vectronic Aerospace Gmbh, Berlin, Germany) linked to satellites (Iridium Communications, McLean, VA). All individuals collared were located by searching roads for tracks, however given the high density of roads in the area it is expected that our sample population is representative of all cougars in the area and not the bolder individuals. Age classes were: kitten (<18 months), subadult (18-24 months), and adults (> 24 months) (Ruth et al., 2011). Procedures followed the Canadian Council on Animal Care (CCAC 2003) and the Alberta Wildlife Animal Care Committee Class Protocol #12 (Research Permit #58627). GPS locations were recorded every 7 hours and A two-sample t-test was used to compare inter-sex monitoring duration. I used location data to identify and locate nursery sites to determine number of offspring and monitor survival.

1.2.3 Survival Analysis – Survival estimates were determined annually and seasonally using Kaplan-Meier models. To assess seasonal variation in survival I defined three seasons: winter (Nov – Mar), summer (Apr – Oct), and hunting season, completely nested within the winter season (Dec– Feb) (Girard et al., 2013; Smereka et al., 2020). The hunting season opened December 1 in all CMAs but closed on different dates for each sex as quotas were filled, and hunting stopped. The hunting season was a subset of the winter season and began December 1 and when the harvest ended, the CMA was then considered in the winter season. If quotas were unfilled, the hunting season closed at the end of February. Alberta also has a fall cougar hunting season in certain Wildlife Management Units that prohibits the use of dogs from September 1 – March 31, however no cougars were harvested during this time and was not examined as part of the hunting season. Intra-sex sources of mortality were examined for adults while kittens were pooled by sex for mortality on the assumption of similar mortality risk. Sources of mortality between adults were compared using exact logistic regressions in R (Zamar et al., 2007) to determine differences in risk of mortality sources.

Birthdate of kittens was estimated from movement data of collared females (based on revisitation of a location subsequently verified as a nursery site), was accurate to within a few days and was used to age those individuals (Clark et al., 2015). Some kittens were marked with numbered ear tags allowing identification at a later age and collars were applied when kittens were older. Kittens were only tagged if the ear was stiff enough to ensure it would not fold from the tags (ca. 3 weeks old). Littermates were assumed to have dependent fates because they are equally at risk if the mother died or when left unattended while the mother was hunting (Ruth et al., 2011).

1.2.4 Cox Proportional Hazard Analysis - Potential hazards (biological and environmental variables) were examined within each sex using a series of univariate Cox proportional hazard models with the Anderson-Gill model for staggered entry in the statistical program R (Johnson et al., 2004; Clark et al., 2015; Therneau, 2021). Hazard ratios approaching 1 (0.99 – 1.001) were considered not be biologically insightful as they signified a minute change in hazard.

Environmental variables with multiple buffer layers examined were incorporated into candidate models and the model for each variable with the lowest Akaike's information criterion adjusted for small sample size (AICc) was used in each season (Burnham et al., 2010).

1.2.5 Biological Covariates - Individual covariates were age class and sex with adult females separated into two classes based on reproductive status: females with and without dependent offspring. Number of dependent offspring was also measured for females and were determined by visiting dens of females suspected of having offspring based on movement data and counting kittens present.

Home range fidelity was investigated as a biological variable by examining whether a mortality event occurred within the previous year's home range or outside of it. For each individual where a mortality event occurred, the previous year's home range was determined using the 95% fixed kernel density in R (Calenge, 2006; Ruth et al., 2011).

Step length (i.e., the distance between consecutive locations) and crossing rates of linear features and roads were examined to calculate associated mortality risk. Linear features included powerlines, pipelines, cutlines, seismic lines, and railways (Canada, 2017, 2018, 2020b). Crossing of roads was examined, but not in the linear features category and were classified as primary (paved) or secondary (unpaved). Roads were separated from other linear features as the potential hazards and use of roads may differ from other linear features. The linear features and roads were mapped in ArcGIS (Environmental Systems Research Institute, Redlands, CA) and the individual crossing rate was determined as crossings/step.

1.2.6 Environmental Variables – Landcover classifications were at 30 m resolution and used the classification from the source as open area, forested area, wetland, agriculture land, edge area, and water (Canada, 2019, 2020a; Li et al., 2020). Forested areas were classified as coniferous, broadleaf, and mixed forests separately. Landcover was modeled as an annual hazard with forest types separate, as well as pooled together, "Forest Pooled", the model with the lower AIC_c was then used in all subsequent time frames investigated. Edge area was classified as any forest cell that borders any other cell type (e.g., open area, wetland), edge area was mapped by buffering 25 m into the forest cell and adjacent cell and removing this area from the original classification. Open area had no vegetation or vegetation ≤1 m tall and consisted of non-vegetated land, grassland, and herbaceous land (Holmes & Laundré, 2006; Canada, 2020a). Forest type layers were acquired from Canadian Forest Service Earth Observation for Sustainable Development of Forest from 2015 with 30 m pixel resolution generated using Landsat data (Canada, 2019). Within ArcGIS a digital elevation model was used to determine elevation, terrain ruggedness and slope (Altalis, 2018). From each GPS point a 300 m radius was created and within these radii the mean elevation (m) and terrain ruggedness (vector ruggedness measure, VRM) was determined (Sappington et al., 2007; Boulanger et al., 2013). Slope (%) was determined using the *Slope* tool in ArcGIS, calculated as the maximum change in elevation between the cell and its neighboring cells. Time since the last snowfall was determined as a metric for hunters ability to detect tracks. Historical weather data was acquired from nine nearby weathers stations (i.e., Breton Plots, Fort Assiniboine, Goose Mountain Lookout, James River Ranger Station, Little Paddle Headwaters, Mayerthorpe, Nordegg, Rocky Mountain House, and Violet Grove) from the Alberta Climate Information Services (ACIS, 2020). Each location was assigned to the nearest weather station and the time difference between the location and the most recent snowfall was determined.

Density and distance from cougar locations were determined for both primary and secondary roads. From each collar point within a 300 m radius road density (km of road) and a 1 km radius building density were determined. The density of roads, residential and industrial buildings (annually, seasonally, fine scale) were then used as covariates (Boulanger & Stenhouse, 2014).

Euclidean distances to forest edge, water, primary and secondary roads, residential and industrial buildings were determined for each cougar location using the *Near* tool in ArcGIS. Closer locations were expected to have more of an effect than those further, to account for this I created exponential decay layers ($e^{(-d/a)}$), where *d* was the distance to the feature and *a* was the buffer value (Nielsen et al., 2009; Smereka et al., 2020). I created layers with buffer radii of 30 m, 50 m, and 100 m for forest edge and water bodies following Smereka et al. (2020). For primary and secondary roads, as well as residential and industrial buildings, exponential decay layers with buffer radii of 50 m, 100 m, 150 m, 200 m, and 250 m were used. A large range of buffer layers were examined to account for cougars response to anthropogenic areas as well as human access to these areas (Banfield et al., 2020). Buffer layers were created, and Euclidean distances were measured using the *Buffer* and *Near* tool in ArcGIS. Each features buffer layers were than ranked using Cox proportional hazard models as an annual hazard and the lowest AIC_c for each layer was than used in each seasons analysis (Knopff et al., 2014). I considered all models within 2 ΔAIC_c of the top model to be comparable (Elbroch et al., 2015).

1.3 Results

Between 2016 – 2021 87 cougars were collared (60 females and 27 males) and monitored for a total of 1158 cougar months (Appendix 1, Table A1.1, Figure A1.1). Of the females collared, we followed 18 litters throughout the study. No significant difference in survival was found between females with and without offspring, or response to potential hazards (Appendix 1, Figure A1.2) so all females were pooled. Mean time monitored was 13.3 months (SE= 1.2, range

= 0.4 – 48.2) and did not differ significantly between males ($\bar{X}$ = 11.0. months, SE = 1.5, range = 0.6 – 35.1) and females ($\bar{X}$ = 14.3 months, SE= 1.6, range = 0.4 – 48.2) (t = 1.99, P = 0.12, df = 85). Of the 87 cougars monitored, 41 were known to have died by the end of the study with 39.0% (16/41) by legal harvest and 19.5% (8/41) from incidental trapping as the two main sources of mortality (Table 1.1).

Table 1.1. Sex-specific causes of mortality for cougars monitored by satellite telemetry in west central Alberta, 2016-2021. Kittens of both sexes were compiled into a single "Kitten" category. Natural factors include predation, disease, and starvation.

	Legal	Illegal	Problem	Landowner	Incidental Trapping	Roadkill	Natural	Unknown	Total
Female	6	3	1	1	5	2	7	1	26
Male	7	0	1	0	3	0	0	0	11
Kittens	3	0	0	0	0	0	0	1	4

I was unable to detect a difference in mortality risk for adults (P = 1.0) by sex, however, males were significantly more likely (P = 0.47) to be legally harvested than females but when all harvest is considered (legal and illegal) males were not more likely (P = 0.23) than females to be harvested. Natural mortalities included predation, disease, and starvation, and did not differ significantly by sex although it was only recorded for females (P = 0.09). There were 3 adult females killed by wolves, 2 of which had dependents. Only 2 females died from vehicle collisions and the likelihood of this mortality source did not differ significantly between sexes (P = 1.0). Of the 11 kittens followed, 4 died and 3 of those were by legal harvest, each <1 month from moving into the subadult age class.

I was able to determine the previous year's home range of 15 individuals and 3 died outside of that established home range. Fidelity to home range did not appear to influence the mortality risk. Individuals with mortality events that were not included did not have enough points in the previous year to determine their home range.

1.3.1 Survival Estimates

Kaplan-Meier models were unable to detect a difference in survival estimates for males and females between adults and subadults annually or within any season (95% CIs overlapped) (Table 1.2). There were no significant changes detected in survival rates between the seasons within either sex although the highest mortality for both males and females was during the hunting season, followed by winter (Table 1.2). Kitten survival was not different annually or seasonally from the other age classes and also had the highest mortality in the hunting season but survival did not differ by season.

Table 1.2. Kaplan-Meier survival estimates and 95% confidence intervals of annual, summer (Apr – Oct), winter (Nov – Mar), and hunting (Dec – Feb) season for collared cougars in Alberta, 2016-2021.

Sex / Age Class	N	Annual		Summer		Winter		Hunting	
		Survival	CI	Survival	CI	Survival	CI	Survival	CI
Kittens	11	0.360	0.121 - 1	1	1 - 1	0.900	0.732 - 1	0.400	0.137 - 1
Male									
Subadult	7	0.857	0.633 - 1	1	1 - 1	1	1 - 1	0	NA[a]
Adult	23	0.586	0.406 - 0.845	1	1 - 1	0.827	0.685 - 0.999	0.591	0.323 - 1.0
Female									
Subadult	14	0.857	0.692 - 1	1	1 – 1	0.929	0.803 - 1	0.667	0.300 - 1
Adult	53	0.628	0.512 - 0.770	0.937	0.879 - 0.999	0.726	0.578 - 0.913	0.649	0.422 - 0.997

[a] All but one individual was censored and the remaining individual died.

1.3.2 Cox Proportional Hazard Analysis

Within the potential hazards investigated, all 5 of the biological covariates significantly influenced survival in at least one season. For the environmental variables, 2 potential hazards, elevation and distance to edge, had poor model fits in all seasons. For anthropogenic variables, 5 potential hazards had poor model fits in every season: density of industrial areas, density of roads (primary and secondary), distance to industrial areas, and distance to primary roads. All other environmental and anthropogenic variables were significant in at least one season.

The Cox hazard model had better fit when forested areas were pooled (Forest Pooled) compared to the model with separate forest types (Forest Separate) (ΔAIC_c 2.22) (Appendix 1, Table A1.2). Of the variables with multiple buffer layers, the distances to forest edge, distances to water, distances to primary roads, and distances to industrial buildings were all within 2 Delta AIC_c, the lowest AIC_C was used. Edge 50 m, Water 100 m, Primary Road 50 m, and Industrial 100 m were used. Distance to secondary roads and residential areas had more pronounced differences between the various buffer layers with Secondary Road 50 m and Residential Distance 100 m as the top hazard models.

1.3.3 Annual Hazards

Sex had a marginally good model fit annually (LR $P = 0.07$) (LR = Likelihood ratio test) but showed no significant risk (HR = 0.54, P $|z|= 0.107$). Even though males and females had the same level of risk, the hazards they faced differed. For males, we found 10 significant variables that were associated with annual risk (Table 1.3). Of the biological variables, increasing crossing rates of secondary roads and linear features both significantly increased risk.

Within the environmental variables season, landcover, water distance, secondary road distance, and residential density and distance all influenced annual survival for males. Hunting season had the highest mortality risk, followed by winter. Males had significantly decreased risk in both agricultural areas and water areas but a significantly increased risk in open areas and wetlands. Additionally, distance from water was a marginally good fit and a moderate significance that increasing distance from water was an increased hazard. Increasing proximity to secondary roads increased risk, as did proximity and density of residential buildings.

Table 1.3. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for annual male cougar survival in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	0.09†	-	-
Kitten		6.2	0.218
Subadult		1.2	0.901
Step Length	0.7	-	-
Primary Road Crossing Rate	**0.02***	2.1E-68	0.317
Secondary Road Crossing Rate	**0.009***	3.9	**0.043***
Linear Feature Crossing Rate	**0.03***	1.2	0.098†
Environmental Variables			
Season	**2E-05***		
Hunting		1.1E09	**2E-16***
Winter		3.0E08	**2E-16***
Landcover	0.08†		
Agriculture		2.4E-07	**< 2E-16***
Forest Edge		1.3	0.721
Open		8.9	**0.006***
Shrubland		2.9	0.226
Water		2.4E-07	**< 2E-16***
Wetland		11.9	**0.035***
Elevation	0.8	-	-
Slope	0.3	-	-
Ruggedness	0.4	-	-
Time Since Snow	**0.01***	0.998	**0.003***
Industrial Density	0.5	-	-
Residential Density	**0.05***	1.1	**3.0E-04***
Primary Road Density	0.8	-	-
Secondary Road Density	0.5	-	-

Water Distance	0.1†	0.01	0.065†
Edge Distance	0.9	-	-
Primary Road Distance	0.8	-	-
Secondary Road Distance	**0.005***	7.2	**0.005***
Industrial Distance	0.5	-	-
Residential Distance	**0.01***	16.9	**0.004***

*Bolded - Significant values
† Marginally significant values

For females, we found 8 variables that significantly affected annual survival (Table 1.4). Of the biological variables, females had significantly increased risk with increased crossing rates of secondary roads and marginally significant increased risk with higher rates of linear feature crossings. Females also had a significantly increased risk with higher primary road crossing rates, but it was only a marginally good model fit. Within the environmental variables season, secondary road distance, residential distance, and residential density also influenced survival. Hunting season, followed by winter had the highest risk for females. Closer distances to both secondary roads and residences also increased risk, as well as higher densities of residences.

Table 1.4. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for annual female cougar survival in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	0.6	-	-
Dependents	0.6	-	-
Litter size	0.6	-	-
Step Length	**0.04***	1.000	**9.64E-05***
Primary Road Crossing Rate	0.1†	1.3E26	**0.0428***
Secondary Road Crossing Rate	**0.005***	6.403	**0.0008***
Linear Feature Crossing Rate	**0.003***	1.3	**0.0027***
Environmental Variables			
Season	**5E-04***		
Hunting		11.7	**5.62E-04***
Winter		5.8	**0.00637***
Landcover	0.6	-	-
Elevation	0.7	-	-
Slope	0.6	-	-
Ruggedness	0.1	-	-
Time Since Snow	**0.02***	0.999	0.112

Industrial Density	0.4	-	-
Residential Density	**0.02***	1.1	**4.67E-04***
Primary Road Density	0.5	-	-
Secondary Road Density	0.3	-	-
Water Distance	0.3	-	-
Edge Distance	0.4	-	-
Primary Road Distance	1	-	-
Secondary Road Distance	**0.02***	3.655	**0.0101***
Industrial Distance	0.6	-	-
Residential Distance	**5E-04***	17.9	**2.81E-04***

* Bolded - Significant values
†Marginally significant values

1.3.4 Seasonal Hazards

In summer, females had increased mortality risk compared to males. No males died in summer however, and the model fit for sex was only marginally significant. Because no males died in the summer, hazard models could only be run on females. Female survival was highest in summer and few variables showed a significant risk (4/22) (Table 1.5). Females only showed significance in one biological variable, an increased hazard to increasing primary road crossing rates. For environmental variables proximity and density of residences, and distance to secondary roads were significant. In terms of distance to residential areas, proximity was a good fit and density was a marginally good fit, finding significantly increased risk with closer proximities and increased densities. Distance to secondary roads was a marginally good model fit and had a moderate significance of increased risk at closer proximities.

Table 1.5. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for survival of female cougars in the summer season in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	0.7	-	-
Dependents	0.2	-	-
Litter size	0.2	-	-
Step Length	0.2	-	-
Primary Road Crossing Rate	**0.04***	3.6E66	**0.0177***
Secondary Road Crossing Rate	0.7	-	-

Linear Feature Crossing Rate	0.4	-	-
Environmental Variables			
Landcover	0.2	-	-
Elevation	0.8	-	-
Slope	1	-	-
Ruggedness	0.9	-	-
Time Since Snow	0.8	-	-
Industrial Density	0.6	-	-
Residential Density	0.1†	1.2	**0.0025***
Primary Road Density	0.8	-	-
Secondary Road Density	0.7	-	-
Water Distance	0.6	-	-
Edge Distance	0.3	-	-
Primary Road Distance	0.8	-	-
Secondary Road Distance	0.1†	7.1	0.065†
Industrial Distance	0.7	-	-
Residential Distance	**0.02***	47.4	**0.0028***

* Bolded - Significant values
†Marginally significant values

We found 6 variables that significantly influenced male survival in winter (Table 1.6). For biological variables increased crossing rates of secondary roads and linear features both significantly increased risk. Within the environmental variables reduced slope, residential density, and proximity to residences and secondary roads all increased risk.

Table 1.6. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for survival of male cougars in winter in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	0.4	-	-
Step Length	0.3	-	-
Primary Road Crossing Rate	0.1†	3.4E-100	0.275
Secondary Road Crossing Rate	**0.004***	15.4	**0.042***
Linear Feature Crossing Rate	**5.0E-04***	1.6	**0.0003***
Environmental Variables			
Landcover	0.3	-	-
Elevation	0.4	-	-
Slope	**0.04***	0.53	0.055†
Ruggedness	0.3		
Time Since Snow	0.1†	1.0	**0.018***
Industrial Density	0.7	-	-
Residential Density	**0.01***	1.2	**0.0004***

Primary Road Density	0.9	-	-
Secondary Road Density	0.9	-	-
Water Distance	0.2	-	-
Edge Distance	1	-	-
Primary Road Distance	0.7	-	-
Secondary Road Distance	**0.02***	12.8	**0.016***
Industrial Distance	0.8	-	-
Residential Distance	**3E-04***	99.5	**1.18E-05***

* Bolded - Significant values
†Marginally significant values

For females we found 6 variables that significantly influenced risk in winter (Table 1.7). Within the biological variables, increasing crossing rates of primary and secondary roads and linear features all significantly increased risk, however, secondary road crossing rate was only a marginally good model fit. For the environmental variables lower ruggedness, and closer proximity to secondary roads all significantly increased risk. Ruggedness was only a marginally good model fit and this was the only instance where it was significant.

Table 1.7. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for survival of female cougars in winter in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	0.5	-	-
Dependents	0.5	-	-
Litter size	0.6	-	-
Step Length	0.2	-	-
Primary Road Crossing Rate	**0.02***	0.0	**< 2E-16***
Secondary Road Crossing Rate	0.06†	5.1	**0.0169***
Linear Feature Crossing Rate	**0.002***	1.4	**2.27E-07***
Environmental Variables			
Landcover	0.9	-	-
Elevation	0.2	-	-
Slope	0.7	-	-
Ruggedness	0.09†	0.0	**0.0154***
Time Since Snow	0.09†	0.99	**0.0361***
Industrial Density	0.8	-	-
Residential Density	0.2	-	-
Primary Road Density	0.7	-	-
Secondary Road Density	0.6	-	-

Water Distance	0.3	-	-
Edge Distance	0.8	-	-
Primary Road Distance	0.6	-	-
Secondary Road Distance	**0.04***	4.8	**0.0242***
Industrial Distance	0.2	-	-
Residential Distance	0.8	-	-

* Bolded - Significant values
†Marginally significant values

Mortality risk was highest for both sexes during the hunting season, yet sex-specific hazards were found. For males, 3 variables influenced survival (Table 1.8). Age class was the only significant biological variables and had increased risk in kittens and subadults. Of the environmental variables, landcover was significant and open areas had a significantly increased hazard, while agriculture areas and water had significantly reduced hazards. Wetlands in the hunting season also showed a significantly increased hazard, however, only 5 location positions were classified as being in a wetland. Distance to secondary roads was also significant, with higher risk at closer proximities.

Table 1.8. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for survival of male cougars in the hunting season in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	**0.001***		
Kitten		76.0	**1.49E-05***
Subadult		7.0	0.0751†
Step Length	0.1†	1.0	0.0613†
Primary Road Crossing Rate	0.9	-	-
Secondary Road Crossing Rate	0.1†	3.6	0.132
Linear Feature Crossing Rate	0.9	-	-
Environmental Variables			
Landcover	0.08†		
Agriculture		1.2E-07	**< 2E-16***
Forest Edge		1.3	0.805
Open		19.0	**7.0E-04***
Shrubland		3.5	0.277
Water		1.2E-07	**< 2E-16***
Wetland		1.2E-07	**< 2E-16***

Elevation	0.7	-	-
Slope	0.8	-	-
Ruggedness	1		
Time Since Snow	0.5	-	-
Industrial Density	0.6	-	-
Residential Density	1	-	-
Primary Road Density	0.8	-	-
Secondary Road Density	0.2	-	-
Water Distance	0.2	-	-
Edge Distance	0.8	-	-
Primary Road Distance	0.5	-	-
Secondary Road Distance	**0.03***	6.9	**0.032***
Industrial Distance	0.6	-	-
Residential Distance	1	-	-

* Bolded - Significant values
†Marginally significant values

Females also had few variables affecting survival in the hunting season compared to other seasons. Five variables were significant, 3 of which were biological variables (Table 1.9). Having offspring was not a significant hazard for females and was a poor model fit but the number of offspring was a marginally good model fit and was significant. Having two or three dependent offspring significantly reduced a female's hazard, whereas three individuals had 4 offspring concurrently, and it was not a significant change in risk from having no offspring. The other significant biological variables were increasing crossing rates of secondary roads and linear features which significantly increased mortality risk. For environmental variables, only increasing residential density and proximity significantly increased risk.

Table 1.9. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for survival of female cougars in the hunting season in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	0.3	-	-
Dependents	0.4	0.46	0.505
Litter size	0.1†	-	-
2		1.8E-08	**< 2E-16***
3		1.8E-08	**< 2E-16***

4		5.3	0.205
Step Length	**0.05***	1	**6.61E-04***
Primary Road Crossing Rate	0.7	-	-
Secondary Road Crossing Rate	**0.006***	4.4721	**3.1E-04***
Linear Feature Crossing Rate	**0.02***	1.2185	**0.0083***
Environmental Variables			
Landcover	0.9	-	-
Elevation	0.3	-	-
Slope	0.2	-	-
Ruggedness	0.4	-	-
Time Since Snow	0.3	-	-
Industrial Density	0.7	-	-
Residential Density	0.08†	1.2	**0.0332***
Primary Road Density	0.8	-	-
Secondary Road Density	0.3	-	-
Water Distance	0.4	-	-
Edge Distance	0.3	-	-
Primary Road Distance	0.4	-	-
Secondary Road Distance	0.4	-	-
Industrial Distance	0.9	-	-
Residential Distance	**0.01***	68.5	**1.88E-06***

* Bolded - Significant values
†Marginally significant values

1.3.5 Fine Scale Hazards

In the 48hrs before death, 3 variables significantly influenced male survival (Table 1.10). Age class was the only biological variable and showed higher risk for kittens and subadults than adults. For environmental variables, landcover showed wetlands, open areas, and shrubland all significantly increased risk, whereas agriculture areas significantly lowered risk. Proximity to secondary roads was also significant, with increased risk at closer proximities. Females had no biological variables significantly influencing mortality risk at the fine scale, but 2 environmental variables did (Table 1.11). Increasing residential density and closer proximity to secondary roads both significantly increased mortality risk.

Table 1.10. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for survival of male cougars 48 hours before death in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	0.1†	-	-
Kitten		4.6	**0.0155***
Subadult		3.4	**0.0362***
Step Length	0.5	-	-
Primary Road Crossing Rate	1	-	-
Secondary Road Crossing Rate	0.06†	0.24	0.121
Linear Feature Crossing Rate	0.2	-	-
Environmental Variables			
Landcover	**0.02***		
Agriculture		1.9E-07	**< 2 E-16***
Forest Edge		0.7	0.620
Open		3.8	**0.0246***
Shrubland		3.5	**0.0322***
Water		NA	NA
Wetland		141.8	**1.42E-06***
Elevation	1	-	-
Slope	0.5	-	-
Ruggedness	0.8	-	-
Time Since Snow	0.4	-	-
Industrial Density	0.4	-	-
Residential Density	0.3	-	-
Primary Road Density	1	-	-
Secondary Road Density	0.9	-	-
Water Distance	0.3	-	-
Edge Distance	0.6	-	-
Primary Road Distance	1	-	-
Secondary Road Distance	**0.05***	3.7	**0.0177***
Industrial Distance	0.3	-	-
Residential Distance	1	-	-

* Bolded - Significant values
†Marginally significant values

Table 1.11. Cox proportional hazard model and likelihood ratio tests for biological and environmental variables for survival of female cougars 48 hours before death in western central Alberta. LR = Likelihood ratio, HR = Hazard ratio.

Biological Variables	LR P	HR	P |z|
Age Class	0.3	-	-
Dependents	0.5	-	-
Litter size	0.8	-	-
Step Length	0.8	-	-
Primary Road Crossing Rate	0.4	-	-

Secondary Road Crossing Rate	0.8	-	-
Linear Feature Crossing Rate	1	-	-
Environmental Variables			
Landcover	0.5	-	-
Elevation	0.7	-	-
Slope	0.9	-	-
Ruggedness	0.4	-	-
Time Since Snow	0.8	-	-
Industrial Density	NA	-	-
Residential Density	**0.03***	1.1	**2.19E-05***
Primary Road Density	NA	-	-
Secondary Road Density	0.6	-	-
Water Distance	0.7	-	-
Edge Distance	0.6	-	-
Primary Road Distance	0.6	-	-
Secondary Road Distance	**0.05***	3.1	**0.0273***
Industrial Distance	0.4	-	-
Residential Distance	0.2	-	-

* Bolded - Significant values
†Marginally significant values

1.4 Discussion

Human harvest and kills of depredating large carnivores often results in mortality that is higher than natural sources (Lee et al., 2005; Holmes & Laundré, 2006; Boulanger et al., 2013; Chakrabarti et al., 2022). Areas that use sport hunting to manage populations frequently have harvest as one of the main mortality sources and due to preferential harvest of males, their survival is often lower than females (Czetwertynski et al., 2007; Robinson et al., 2008; McKinney et al., 2009; Ruth et al., 2011). We found hunting to be the highest cause of mortality and collared males were more likely to be legally harvested but were unable to detect a difference in survival between males and females. Mortality associated with legal harvest was low at 39% in our study compared to some other areas (e.g., 62 to 75%) (McKinney et al., 2009; Wolfe et al., 2015) but harvest mortality rates vary widely and areas with lower harvest rates (e.g., 25%) have found male survival lower than females (Ruth et al., 2011). When both illegal and legal harvest were examined, proportions of male and females harvested did not differ, no difference in harvest rates could account for not finding female survival significantly higher than males.

While survival estimates between sexes did not differ, we found that both biological and environmental variables influencing male and female cougar survival differed significantly. Of the variables affecting male annual survival, 6 also affected female annual survival: secondary and linear feature crossing rate, residential density and distance, secondary road distance, and season. Additionally, male annual survival was affected by age class, landcover, and distance to water. Male kitten survival is typically 0.46 – 0.66 (Logan & Sweanor, 2001; Lambert et al., 2006; Ruth et al., 2011), but our survival estimate was lower, and may be due to our small sample size. Subadults in our study showed a higher hazard in comparison to adults, which we attributed to the risk of dispersing into new habitats. In many large carnivores, subadult males disperse farther than females and more frequently leave their natal ranges (McLellan & Hovey, 2001; Stoner et al., 2013). Subadult and adult cougars differ in their movements, primarily due to subadults dispersing into new environments whereas adults have an established home range (McLellan & Hovey, 2001; Morrison et al., 2015). Interspecific aggression can force dispersing cougars into lower quality, potentially more dangerous habitats, as well as being naïve to the hazards present within novel habitats (McKinney et al., 2009; Thorsen et al., 2022).

Large carnivore survival can be affected by landscape features with areas closer or easier to access by humans lowering survival (Nielsen et al., 2004b; Ruth et al., 2011; Boulanger et al., 2013). Similarly, our analyses found that landcover classification only affected annual survival of males. Open areas were a higher risk habitat than other landcover types which was expected, presumably due to hunters having better visibility of tracks and being more easily accessible (Nielsen et al., 2004b; Ruth et al., 2011; Boulanger et al., 2013). Roads were commonly bordered by open areas (shoulders of road, ditch) and these open areas could be used to spot tracks from cougars crossing that have been distorted on the road itself by traffic. The higher proportion of males harvested supports this, while no difference in proportions harvested legally or illegally suggests females could be killed opportunistically rather than actively hunted and therefore landcover classification did not significantly affect female survival. Further, while agriculture areas and distance to water affected male annual survival, with closer proximities having lower risk, these variables were not significant for females. Agricultural areas could lower risk from harvest because large connected agricultural areas are harder for hunters to access because permission from multiple landowners would be required.

The only variable that significantly affected female annual survival that did not affect males was the increased risk associated with higher primary road crossing rates. The hazard ratios associated with primary road crossing rates (i.e., E-100 – E66) appear inflated because they were rarely used but still identify significant hazards. While male cougars can have higher primary road crossing rates, females had higher road densities within their home ranges (Schwab & Zandbergen, 2011) (Appendix 1, Table A1.3). Because females in our study were not more likely to be hit by vehicles, the increased risk could be associated with indirect mortality factors. In a lower quality habitat individuals may need to exploit more dangerous resources including residential areas resulting in problem animal kills or landowner kills, they may also succumb to natural factors like starvation (Basille et al., 2013). Alternatively, females have smaller home ranges and tracks found on roads used for hunting have a greater chance at resulting in a successful hunt (Keehner et al., 2015; Azevedo et al., 2020). Further analysis of inter-sexual difference in home range characteristics of cougars in our study area could provide insights on road densities effect on movement and risk.

Hazard analyses showed that significant variables varied seasonally. Some variables were expected to increase risk during the hunting season, but instead were found to increase risk during the non-hunting winter season. In winter, the main cause of mortality was incidental trapping, which has been documented in large carnivores within areas that allow trapping of other species and can result in non-fatal or fatal injuries depending on the traps used and the non-target species caught (Knopff et al., 2010b; Andreasen et al., 2018; Lamb et al., 2022). While crossing rates of secondary roads, linear features, and time since snowfall were all expected to increase risk during the hunting season by allowing easier access by hunters and detection of fresh tracks, instead we found significance during winter. These variables would have the same effect on trappers as they do hunters, allowing easier access and knowledge on where to set traps. Instead of finding these variables were significant in the hunting season due to harvest risk, I found they increased risk in the winter due to incidental trapping. Within the study area trapping of wolves is permitted with neck snares and bait piles commonly used. Regulations against using killing neck snares could be put in place for areas that manage cougar sport hunting to reduce this mortality. Additionally, areas that allow traps and snares with carrion bait for permitted species can use flexible harvest quotas to compensate for incidental trapping mortalities from previous years (Knopff et al., 2010b).

The fine time scale was able to distinguish proximate variables resulting in harvest, with significant variables differing for each sex. Ecologically, male and female cougars behave differently, using different landscapes and are exposed to different risks (Kertson & Marzluff, 2010; Schwab & Zandbergen, 2011; Azevedo et al., 2020; Smereka et al., 2020). Combined with the proportionally higher harvest of males, the factors that affect survival within each sex are different. For males, cover and distance to areas where hunters have easier access appeared to have the largest effect on survival with open areas, shrublands, and wetlands all lowering survival with increasing proximity to secondary roads. Highlighting that areas with better visibility to locate and follow tracks become increasingly dangerous in areas that are also easier to access by hunters. Subadults are most at risk during these periods, suggesting that naivety in already hazardous environments may result in riskier actions such as ambivalence to human infrastructure (Thorsen et al., 2022). For females, proximity to humans was the largest factor affecting survival. Females that were closer to residences, as well as those in areas with higher residential densities have increased risk of mortalities.

Future work should prioritize sampling more kittens, subadults, and adult males to better understand the differences to potential hazards. I acknowledge that comparisons between survival estimates, and sources of mortality may be skewed due to small samples of younger age classes and a female dominated sample. While the survival estimates of kittens were below those in other areas (Logan & Sweanor, 2001; Lambert et al., 2006; Ruth et al., 2011), as well as studies in Alberta (Ross & Jalkotzy, 1992), our sample size was small. While Ross and Jalkotzy (1992) found kitten survival rates of 98%, they began monitoring later into the kittens life and likely missed early mortalities. Our study began monitoring earlier, however within our sample, there were only 4 kitten mortalities. Similarly, while our sample size of subadults was larger than kittens, once separated by sex, sample sizes, specifically males, were small. However, the model fit and hazard ratio for age class were both strongly significant lending the analysis support. Additionally, examining sources of mortality would also be beneficial to determine what sources constitute the majority of each sexes mortalities and where each sex is most vulnerable. Females having higher natural mortality rates has been postulated due to intraspecific mortality while defending kittens (Robinson et al., 2008). I found 3 adult females killed by wolves, 2 of which had dependents, supporting the idea that female mortality may be higher due to natural sources while defending kittens, however further analysis would be needed to better understand the risks associated with protecting dependents. Additionally, males were harvested more within our sample, attributed to hunter preference and the use of dogs enabling hunters to selectively target males (Martorello & Beausoleil, 2003). Our study area also has a male biased quota, allowing females to remain and the landscape, producing kittens to help compensate for harvest mortality. Females within our study area are protected while they have kittens, which further lower their harvest. A larger sample of males to examine rates of mortality by different sources in our study area could help determine whether natural mortality is more common in females.

Within our study area, mortality from farmers and ranchers as depredation was not a significant source of mortality, further, agriculture areas had reduced risk. Some ungulates use private land to fulfill part of their habitat requirements (Morehouse et al., 2018), and Smereka et al. (2021) suggested agricultural areas can be used by cougars as a source of prey. The use of agricultural areas for wild prey acquisition should be taken into consideration for areas with higher rates of depredation as rigorous harvesting of cougars that are using agriculture areas to meet nutritional demands could affect cougar populations.

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1.6 Appendix

Table A1.1. Sample size of cougars captured, collared, and monitored in west central Alberta by sex and descriptive statistics of the time frames individuals were monitored between 2016-2021.

	Individuals	Months Monitored	Mean	Median	Standard Deviation
Female	60	860.90	14.30	10.90	12.10
Male	27	297.70	11.00	10.10	7.60
Total	87	1158.50	13.30	10.50	11.00

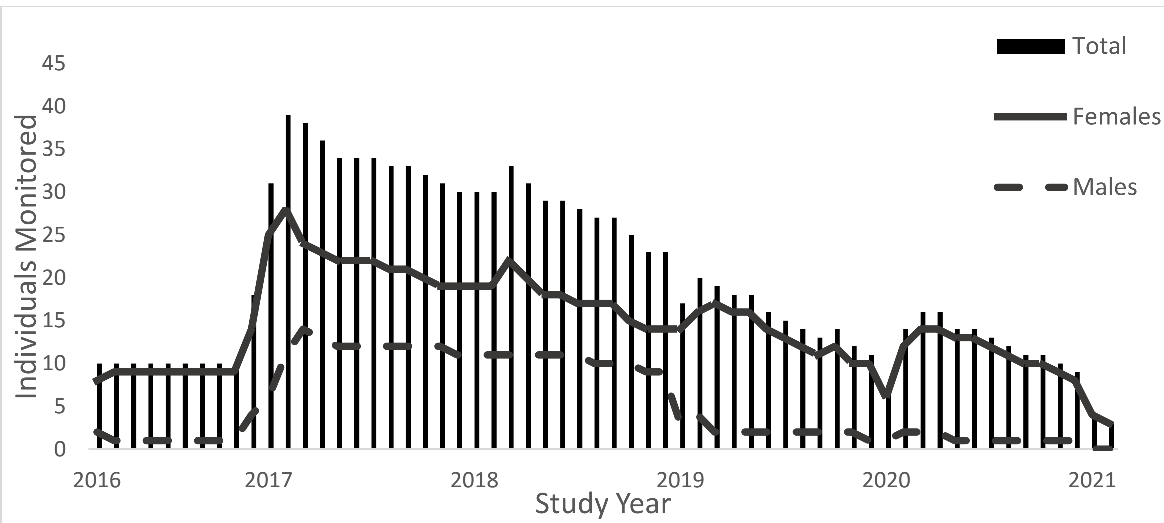

Figure A1.1. Number of individuals monitored at each month of the study in west central Alberta, 2016-2021. A total of 87 cougars were monitored.

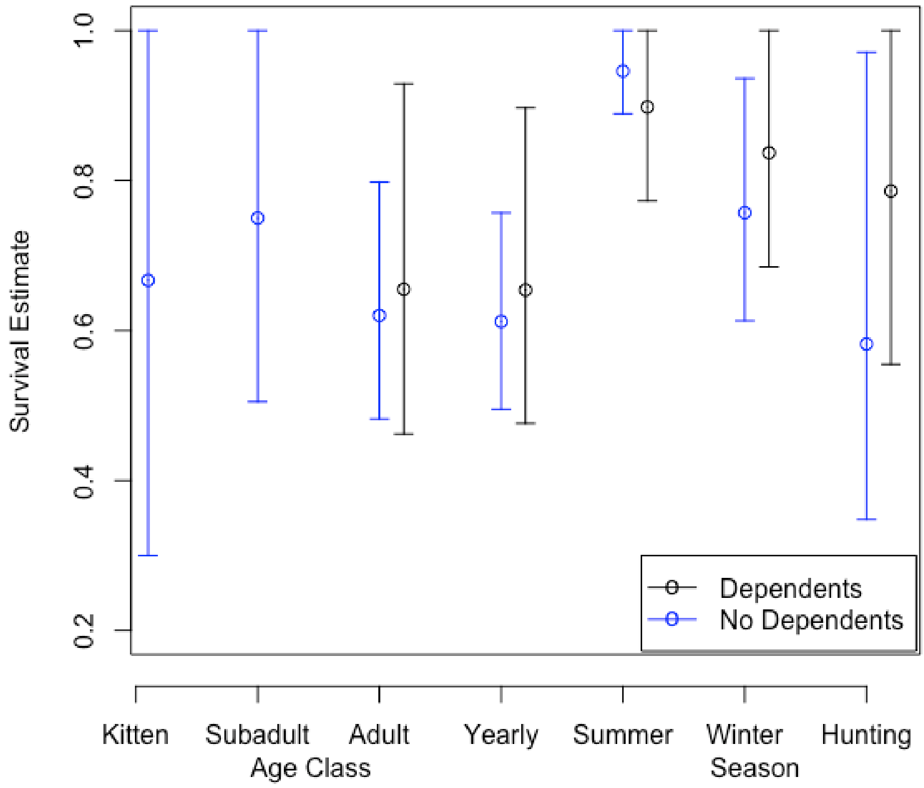

Figure A1.2. Survival estimates for female cougars with and without dependents within west central Alberta between 2016-2021. A total of 60 females were monitored during the study including 18 with offspring.

Table A1.2. Akaike Information Criterion corrected for small sample (AIC_c) size ranking of covariates to be used within the Cox proportional hazards models for cougars within Alberta, 2016–2021.

Classification	AIC_c	Delta AIC_c	AICc Wt.	LL	K
Forest Edge 50m	249.67	0	0.43	-123.83	1
Forest Edge 30m	249.87	0.21	0.39	-123.94	1
Forest Edge 100m	251.39	1.72	0.18	-124.69	1
Water 100m	249.73	0	0.39	-123.86	1
Water 30m	250.15	0.42	0.32	-124.07	1
Water 50m	250.32	0.59	0.29	-124.16	1
Industrial 100m	250.88	0	0.24	-124.44	1
Industrial 150m	251.12	0.24	0.21	-124.56	1
Industrial 50m	251.12	0.25	0.21	-124.56	1
Industrial 200m	251.39	0.51	0.18	-124.69	1
Industrial 250m	251.58	0.71	0.17	-124.79	1
Residential 100m	231.41	0	0.34	-114.71	1
Residential 150m	231.72	0.3	0.29	-114.86	1
Residential 200m	232.14	0.73	0.24	-115.07	1
Residential 250m	234.33	2.91	0.08	-116.16	1
Residential 50m	235.17	3.75	0.05	-116.58	1
Primary Road 50m	248.88	0	0.27	-123.44	1
Primary Road 100m	249.07	0.19	0.25	-123.53	1
Primary Road 150m	249.57	0.7	0.19	-123.79	1
Primary Road 200m	250.01	1.13	0.15	-124.00	1
Primary Road 250m	250.29	1.42	0.13	-124.15	1
Secondary Road 50m	235.5	0	0.89	-116.75	1
Secondary Road 100m	240.46	4.96	0.07	-119.23	1
Secondary Road 150m	243.26	7.77	0.02	-120.63	1
Secondary Road 200m	244.32	8.82	0.01	-121.16	1
Secondary Road 250m	245.1	9.61	0.01	-121.55	1
Forest Pooled	370.91	0	0.75	-179.45	6
Forest Separate	373.13	2.22	0.25	-178.56	8

Table A1.3. Summary statistics of two tailed two-sample t-test examining primary road densities (km) within a 300 m buffer radius of male and female cougar locations.

	Mean	Variance	N	Df	t Stat	P
Males	1.766	1077	27507	114767	2.135	0.0327
Females	2.268	1411	87262	-	-	-