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Resource selection studies are commonly used to assess the landscape features that animals select or avoid in their environment. Selection for certain landscape features and landcover types may vary by sex and reproductive status of an individual, and habitat selection studies should incorporate these factors. Cougars *Puma concolor* are a wide-ranging species that live in a diversity of habitats with varying levels of human disturbance. Geographic positioning satellite telemetry collars were deployed on 55 males, single females and females with kittens. We used a two-stage resource selection function to assess the seasonal habitat characteristics used by adult cougars in west-central, Alberta, Canada, near the northern extent of the species range, from 2016 to 2018. A latent selection difference function was used to compare differences in habitat selction between groups. All groups selected for similar habitat types including edge habitat, close proximity to water, sloped terrain, forested habitat and avoided roads. During the summer, close proximity to water and wetland land cover were among the most selected 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. Selection for slope and avoidance of open agricultural land were among the most important for females with kittens. Our results provide insights into those landscape variables that are important for cougars at the northern extent of their geographical range.

Keywords: cougar, habitat selection, latent selection difference function, puma concolor, reproductive state, resource selection function, season

Understanding how animals use the environment to acquire resources crucial to survival is a fundamental component of wildlife management and conservation. Assessing the relationship between animals and their environment commonly uses resource selection functions (RSF) to determine habitat characteristics which are selected or avoided (Boyce et al. 2002, Manly et al. 2002). Carnivore distribution is ultimately driven by prey (Carbone and Gittleman 2002), but habitat features and human disturbance may influence habitat quality, and prey encounter rate. Understanding large carnivore habitat selection can provide insights into the resources needed for their survival and to help reduce conflict with humans.

The range of cougars *Puma concolor* is the largest of any Western Hemisphere mammal and extends from the Yukon, Canada to southern Chile (Yáñez et al. 1986, Walker et al. 2010, Teichman et al. 2013, Jung et al. 2015, Sunquist and Sunquist 2017). They occupy varied ecosystems from deserts, temperate and tropical rainforests, and areas with harsh winters (Ross and Jalkotzy 1992, Logan and Sweanor 2001, Sunquist and Sunquist 2017, Elbroch and Kusler 2018). Cougars require habitat that provide sufficient large prey, concealment cover and prefer areas with low human development and disturbance (Seidensticker et al. 1973, Koehler and Hornocker 1991). However, cougars have high plasticity (Soria-Díaz et al. 2018) and some live in areas with high habitat fragmentation and human-caused mortality (Knopff et al. 2014). At a finer scale, cougars often hunt, rest and raise offspring in habitats with thick understory (Maehr and Cox 1995, Dickson and Beier 2002). Cougars coexist with other predators (Elbroch and Kusler 2018), and selection for dense vegetation may reflect avoidance

of dominant carnivores instead of selection of high quality habitat (Durant 1998). Within forests, cougars prefer areas near open landscapes and wetlands used by prey, and the transition between habitat types that provide stalking cover (Dickson and Beier 2002, Laundré and Hernández 2003, Cox et al. 2006, Knopff et al. 2014). Cougars may also prefer steep terrain and riparian areas that provide a hunting advantage (Logan and Irwin 1985, Dickson and Beier 2002).

The habitat an animal selects may be influenced by sex and reproductive status, and evaluation of habitat selection should incorporate these factors (Benson and Chamberlain 2007). Because of decreased mobility of females with offspring and high nutritional demand (Logan and Sweanor 2001), differences in habitat selection between female carnivores with and without offspring can be expected (Benson and Chamberlain 2007). Similar to many species, female cougars spend most of their adult life pregnant or raising offspring and require habitat with sufficient resources (Logan and Sweanor 2001). Until six to eight weeks old, kittens remain at the den site and are unable to travel (Logan and Sweanor 2001), restricting the mother's movements (Elbroch et al. 2015). As kittens begin travelling and become more nutritionally demanding, the mother may need to hunt more (Logan and Sweanor 2009). In comparison, solitary cougars with lower energetic demands may hunt less and are unconstrained by offspring mobility (Logan and Sweanor 2001). Males do not contribute to offspring rearing and invest 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, cougar habitat selection may differ between males, females and by reproductive status.

In temperate ecosystems, selected or avoided habitat features change seasonally. Travelling through deep snow is energetically demanding and avoidance of habitats with greater snow accumulation may be beneficial to cougars in winter months (Koehler and Hornocker 1991). Further, prey may change elevations or habitats seasonally to forage, and cougars may follow prey (Telfer 1978, Koehler and Hornocker 1991). Numerous studies have investigated cougar habitat selection (Logan and Irwin 1985, Van Dyke et al. 1986, Belden et al. 1988, Dickson and Beier 2002, Knopff et al. 2014); however, few have investigated how habitat selection is affected by season, sex and reproductive status (Blake and Gese 2016, Yovovich et al. 2020).

We studied habitat selection of cougars in west-central Alberta, Canada, with the goal of assessing habitat selection at the home range scale and then, using the results of a two-step RSF, determining the most important habitat features for independent adult males, adult females and females with kittens for winter and summer at the population level. We assessed the differences in habitat selection between reproductive status and season using a latent selection difference (LSD) function. We predicted that cougars will: 1) use areas within their home range where hunting success will be high, 2) select complex habitats that provide both safety from competing carnivores and hunting opportunities, 3) avoid anthropogenic features, 4) females with kittens will select for areas associated with high hunting success and safety more strongly than other life history groups, 5) habitat selection for single females and males will be similar and 6) habitat selection will change seasonally for all groups.

Material and methods

Study area

The study covered ca 26 205 km² in west-central Alberta, Canada west of the town of Rocky Mountain House and north to Whitecourt, south towards Sundre and the Rocky Mountains to the west (Fig. 1). The area is in the central mixed-wood, lower foothills, upper foothills, subalpine and alpine ecoregions (Natural Regions Committee 2006) and is in the northeastern range of cougars. Logging and hydrocarbon extraction activities are common and have created a network of roads, pipelines and seismic lines. The area transitions from agricultural lands to the east with rolling foothills and mountains to the south and west, and boreal habitat to the north. Forests are dominated by 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 (Inkpen and Eyk 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 has cold winters with heavy snow falls, wet springs and warm summers (Strong 1992, Morgantini and Kansas 2003). Cougar hunting occurs from autumn to late winter in Alberta and the study area covered three cougar management areas.

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. Small prey includes snowshoe hare *Lepus americanus*, beaver *Castor canadensis*, porcupine *Erethizon dorsatum*, red fox *Vulpes vulpes*, ruffed grouse *Bonasa umbellus* and spruce grouse *Falcipennis canadensis*. Cougars may also prey on domestic animals. Other predators include black bears *Ursus americanus*, grizzly bears *U. arctos*, lynx *Lynx canadensis*, wolves *Canis lupus*, coyote *C. latran* and wolverine *Gulo gulo*.

Capture and handling

Location data was obtained from cougars that were captured and fitted with global positioning system (GPS) radio-collars from 2016 to 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⁻¹) and Medetomidine (0.05–0.075 mg kg⁻¹). Once processing was complete cougars were reversed using Atipamezole (0.4 mg kg⁻¹). Vectronics Vertex Lite VHF/GPS radio-collars were fit on cougars and recorded a GPS location every four hours for females and seven hours for males and the data were retrieved via Iridium satellite. Collars were recovered after harvest, natural mortality, recapture or when the rot-away broke down and the collar fell off after two to three years. Age was estimated using gum-line recession, pelage spotting and barring, and tooth
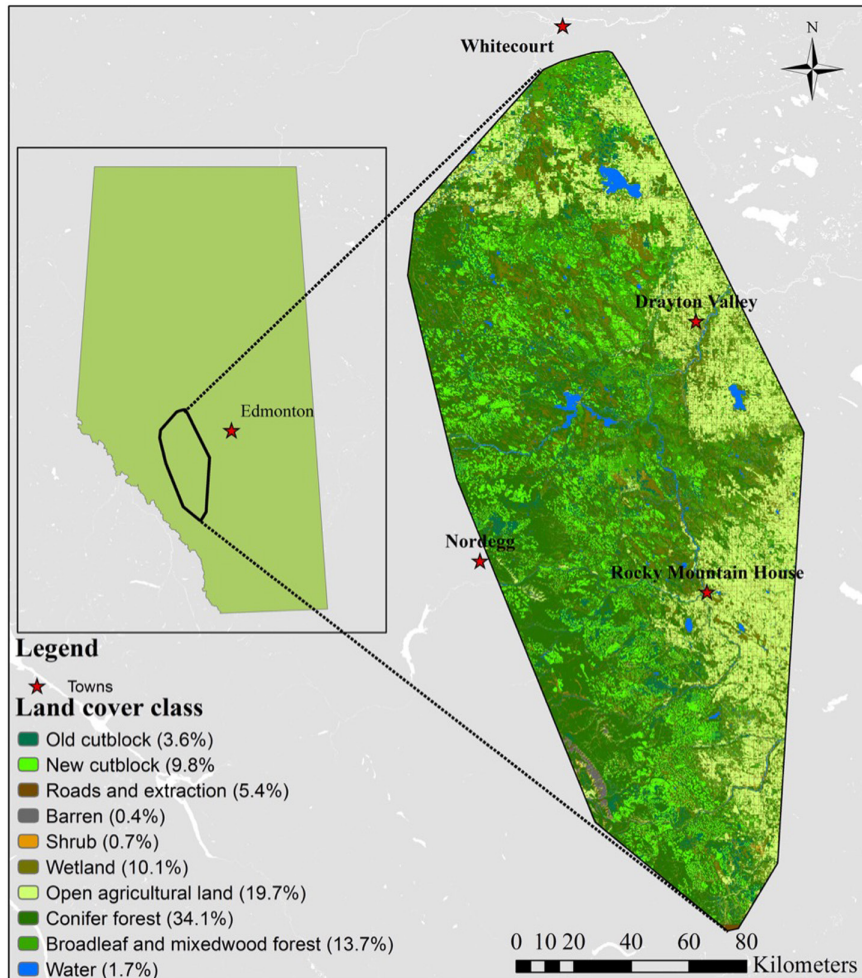
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Figure 1. Study area location with inset showing the 100% minimum convex polygon where cougars were tracked from 2016 to 2018 in west-central Alberta, Canada. Legend indicates the landcover type and the proportion that made up the study area.

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 guidelines on the care and use of wildlife (CCAC 2003). Immobilization and capture procedures may affect animal movement patterns, and although no study has investigated post-capture effects on cougars, we followed Thiemann et al. (2013), and removed the first five days of location data to reduce the effects of handling on habitat use in our analyses.

Data preparation

Only cougars with an established home range were used in the analysis. Young individuals were considered to have an established home range if dispersal movements had completed and/or we verified that their mother or siblings were no longer present. Home range establishment was identified using segmentation analysis (Lavielle 1999) and 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. Individuals with no breaks in a track were considered to have an established home 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. Segmentation analysis and NSD also allowed us to identify if, and when, individuals went on excursions. Long excursions away from their home range were deleted from use locations as we did not consider them part of the individual's home range.

Adult cougars, defined as independent individuals with an established range, were grouped by sex and reproductive status: male, single female and female with offspring. Groupings for females were based on evidence of kittens at the time of collaring and subsequent ground surveys, camera traps at kill sites and den site visits. Once kittens dispersed, females were categorized as single females. We only included females of known reproductive status. We split location data into winter, when snow was on the ground and temperatures were typically below freezing (1 November–31 March), and summer, when green-up had occurred and waterbodies thawed and remained open (1 April–30 October) (Girard et al. 2013). Cougar location data was also analysed using reproductive status, resulting in six 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). Although movement constraints will vary with the age

of kittens, we felt that similar resources would be important for females with kittens of any age.

Habitat covariates

To investigate habitat selection, we included three types of variables which could be important to cougars in Alberta: landcover, topography and human disturbance (Table 1). Landcover data was obtained from the Canadian Service Earth Observation for Sustainable Development of Forest (EOSD) for 2000 using Landsat data with a 25 m pixel resolution (Natural Resources Canada 2009). We used the Alberta Biodiversity Monitoring Institute's human footprint index layer (Alberta Biodiversity Monitoring Institute 2012) to update the EOSD landcover layer with forestry and hydrocarbon extraction activity and road development to match the study period. The landcover dataset was reclassified into nine ecologically relevant landcover types for cougars including old cutblocks (>25 years old; OC), recent cutblocks (≤25 years old; NC), industrial (roads, well-sites, compressor stations; RE), barren (exposed land, rock/rubble; BN), shrub (SB), wetland (herb, shrub and treed wetland classes dominated by black spruce; WL), open agricultural land (OAL), conifer forest (CF) and mixed deciduous forest (broadleaf and mixedwood forest; BMF). The presence of forest may be more important than the type of forest, and we created a forest layer (FOR) by combining all forested landcover types. Cutblock categorization was based on vegetation regeneration stages (Song 2002). Water bodies were not considered available habitat for cougars and were excluded from models. The nine landcover classes were dummy coded (1/0), allowing us to acquire beta coefficients for each class, and perform model selection on a priori models with select classes.

Topographic variables included elevation, slope, terrain ruggedness index (TRI), distance to water and distance to edge habitat. We used a 25 m digital elevation model (AltaLis, accessed 2019) and Spatial analyst in ArcGIS (Environmental Systems Research Institute, Redlands, CA, USA) to develop layers for elevation, slope, aspect and TRI. Elevation for each pixel was obtained from the digital elevation model. 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 cell of the digital elevation model and its eight neighbouring cells and we used this to measure terrain heterogeneity (Riley et al. 1999). Forest edge was defined as the intersection between forest landcover types and all other landcover types (Knopff et al. 2014). Distance to edge was the Euclidean distance from each pixel to forest edge. Distance to water was the Euclidean distance from each pixel to water. Locations close to forest edge or water may have more of an effect on cougars compared to locations further away, so we also derived exponential decay layers for both edge and water. Exponential decay used 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). We 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. 2014).

Table 1. Categorical and continuous landscape variables for cougar habitat selection in west-central Alberta, Canada, 2016–2018. The distance-to or exponential decay layer of the same class (i.e. distance to road, exponential decay of road (170 m)) that had the best model fit based on Akaike information criteria was used in model selection and is indicated with *.

Variable type	Class	Abbreviation	Format 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
Topography	Slope	SLOPE	Continuous
	Elevation (DEM)	ELEV	Continuous
	Terrain ruggedness index (TRI)	TRI	Continuous
Distance measures	Distance to road	DROAD	Continuous
	Exponential decay of road (170 m)*	RD170	Continuous
	Distance to resource extraction	DEXT	Continuous
	Distance to residential areas	DRES	Continuous
	Exponential decay of residential areas (210 m)*	RES210	Continuous
	Distance to edge	DEDGE	Continuous
	Exponential decay of edge (30 m)	ED30	Continuous
	Exponential decay of edge (50 m)*	ED50	Continuous
	Exponential decay of edge (100 m)	ED100	Continuous
	Distance to water (riparian or stagnant)	DWAT	Continuous
	Exponential decay of water (30 m)	WAT30	Continuous
	Exponential decay of water (50 m)	WAT50	Continuous
	Exponential decay of water (100 m)*	WAT100	Continuous

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We used road, well-site, compressor site, pipeline and residential data obtained from the human footprint index to create habitat disturbance layers using the Euclidean distance from each pixel to the nearest feature. We created distance to road, residential, extraction (active well-sites and compressor stations) and also used these layers to create exponential decay layers for road (buffer distance 170 m; RD170), residential (buffer distance 210 m; RES210) and extraction (buffer distance 100 m) (Knopff et al. 2014). Buffer radii were based on distances that affected cougar habitat selection according to the literature. Layers were created in ArcGIS using the distance tool and raster calculator.

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:

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

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, cougars with established home ranges based on NSD and segmentation analysis, had minimum convex polygons (MCP) delineated using the minimum bounding geometry tool in ArcGIS to calculate the habitat available to each cougar (i.e. third order selection; Johnson 1980). Available points were generated at a density of 10 points km^{-2} within a cougar's 100% MCP (Denny et al. 2018). We considered the MCP a suitable measure of availability as it represented each individual's home range, and for our 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. Individual use locations within a group were compared to the available locations within their total home range to determine what habitat variables were selected or avoided by season. Locations on water but close to land were snapped to the nearest landcover type. The majority of the locations on water occurred during summer when cougars were probably using areas adjacent to water and such locations could be due to GPS fix error (5–10 m) or streams smaller than the cell grid size. Location data was screened for errors by calculating velocity of travel for each cougar and removing locations that would be physically impossible to accomplish between locations.

Because model covariates were either binary (i.e. landcover types) or continuous (e.g. slope), we standardized each continuous predictor variable so it had a mean of zero and

standard deviation of one (Gotelli and Ellison 2004). We used the Akaike information criterion corrected for small sample size (AICc) to check each continuous variable for nonlinear fit (i.e. quadratic or natural log transformation) and the form with the lowest AICc was used in the models (Burnham and Anderson 2002). For distance-to variables that also had exponential decay forms, only the variable with the best AICc fit was kept for analysis. Collinear continuous variables that had a Pearson's correlation coefficient of $\geq |0.6|$ were not included in the same model and the more biologically relevant variable was retained. All data were evaluated using variance inflation factor (VIF) and only variables with a VIF < 3 were used in the same model. The most common and widely distributed habitat was conifer forest (CF). Shrub (SB) and barren (BN) landcover types made up <1% of the available points, and were likely to result in perfect predictors, so we grouped conifer forest, shrub and barren into our reference class.

Our modelling approach was to use a priori models to describe cougar habitat selection. We 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 optimistic estimates of standard errors, however, it allowed us to find the top model describing cougar habitat selection for each of the six groups, and identify a model that could be used in the two-step approach. To construct and analyze our six a priori models we used the package *lme4* in R (Table 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. 2014) and field observations while visiting kill sites and den sites. We constructed models for natural habitat, anthropogenic features, safety and a model with variables from each called 'combined'. Animal ID was a random effect in each model to account for autocorrelation and unequal sample sizes of location data (Gillies et al. 2006). The four models plus the null model were tested for each cougar grouping and the model with lowest AICc but > 2 ΔAICc from the top competing model was considered the top model (Burnham and Anderson 2002).

The primary focus of the RSF analysis was to estimate population level habitat selection. A two-step modelling approach was used as it addressed autocorrelation, variability in number of use locations and can fit a generalized linear model (GLM) to individuals (Davidian and Giltinan 1995, Sawyer et al. 2006, Fieberg et al. 2010). Due to variability in landcover type and terrain across the study area (Fig. 3) and variability in sample sizes across individuals, we expected there to be high error rates for some coefficients

Table 2. Candidate resource selection function models use to assess habitat selection of adult cougars during winter and summer in west-central Alberta, Canada, 2016–2018. See Table 1 for acronyms.

Model	No. of covariates	Model structure
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

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(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. The disproportional error rates were addressed using 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).

For the two-step modelling approach, we used the package *amt* in R to fit the top model using the mixed-effects regression to a GLM for each individual in a group (Signer et al. 2019). We 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 not overlapping zero were considered significant for each beta-coefficient. We checked the 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, similar to Takahata et al. (2014).

Latent selection difference

To examine differences in habitat selection between groups, we used a latent selection difference (LSD) function, with one group coded as 1 and the comparison group as 0 (Fischer and Gates 2005, Latham et al. 2013). LSD analyses assumes all animals had similar habitat availability. The same covariates from our top RSF model were used in the LSD. Newey–West variance inflation was used to estimate standard errors (Newey and West 1987, Roever et al. 2014).

We compared differences in seasonal selection (females with kittens in winter (1) × females with kittens in summer (0); single females in winter (1) × single females in summer (0); males in winter (1) × males in summer (0)) and differences in reproductive status and season (females with kittens in winter (1) × single females in winter (0); females with kittens in winter (1) × males in winter (0); females with kittens in summer (1) × single females in summer (0); females with kittens in summer (1) × males in summer (0); single females in winter (1) × males in winter (0); single females in summer (1) × males in winter (0)). For landcover and exponential decay variables, a positive coefficient indicates that the group coded as 1 had stronger selection for the habitat variable than the comparison group, while a negative coefficient indicates that the group coded as 0 had greater selection for the habitat variable. The opposite is true for distance to variables (i.e. distance to resource extraction). Both groups have similar selection for the habitat variable if coefficient error bars overlap zero.

Results

Of the 66 cougars captured that remained in the study area, 11 females had an unknown reproductive status and were excluded from the analysis. There were 58 432 use locations and 207 597 available locations for the 55 cougars. Mean age of females was 4.3 years (range = 2–9 years), and 3.3 years (range = 1.5–5 years) for males. Four females went

on excursions, resulting in 324 use locations (<1%) being removed. For males in winter n = 14 individuals (4654 locations, $\bar{x}$ $\bar{x}$ = 332, range = 54–655); males in summer n = 13 (8687 locations, $\bar{x}$ $\bar{x}$ = 668, range = 101–958); single females in winter n = 32 (12 822 use locations, $\bar{x}$ $\bar{x}$ = 401, range = 25–1396); single females in summer n = 32 (23 547 locations, $\bar{x}$ $\bar{x}$ = 736, range = 95–2212); females with kittens in winter n = 13 (4608 locations, $\bar{x}$ $\bar{x}$ = 316, range = 19–867) and females with kittens in summer n = 13 (4114 locations, $\bar{x}$ $\bar{x}$ = 354, range = 46–912). Of the use locations, 2% (1403 locations) were located on water and snapped to the nearest landcover type. No locations were identified as being biologically impossible.

For our model construction, the natural log forms of TRI, SLOPE, distance to extraction (DEXT) and elevation (ELEV) had the best fit, while the exponential decay forms of edge with a 50 m buffer (ED50), water with a 100 m buffer (WAT100), RES210 and ROAD170 had the best model fit to cougar habitat selection (see Table 1 for variables).

The mixed-effect RSF indicated that the combined model, which included SLOPE, WL, OAL, FOR, ED50, WAT100, RD170 and DEXT was the top model for all six groups of cougars and all had an AICc weight = 1 (Supplementary material Appendix 1 Table A1–A6). Results of the two-step RSF of the combined model (Fig. 2) indicated that the most important variables for cougar habitat selection across groups were edge, proximity to water, forest and slope (Fig. 2, Supplementary material Appendix 1 Table A7). However, selection for forest and edge was not significant for females with kittens in summer and selection for proximity to water was not significant for females with kittens in winter. The six groups also avoided roads, although for females with kittens in both seasons it was not significant. Females with kittens in summer and males in winter also had significant selection for areas close 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 3–5). For males in summer, the most important habitat feature and significantly selected, was proximity to water and wetlands, while in winter, proximity to water and wetlands fell to the third and last ranked variables, respectively (Table 3). During winter, numerous variables affected selection for males but the most important covariates selected for were forested landcover and edge habitats, which were ranked sixth and third most important during summer, respectively. For single females in summer the most important variables selected for were proximity to water and forested landcover, while in winter, both variables were ranked third and first, respectively (Table 4). During winter, the second ranked variable was slope, which was the fourth ranked in summer, and both were significant and selected for. Large differences in magnitude of selection occurred for females with kittens (Table 5). During summer, the most important, significantly selected features were wetlands and proximity to water which were the least important during winter. The highest-ranked features for females with kittens in winter were forested landcover (significantly selected) and open agricultural land (avoided, not significant). During summer, open agricultural land was ranked sixth and forested landcover was ranked seventh and both
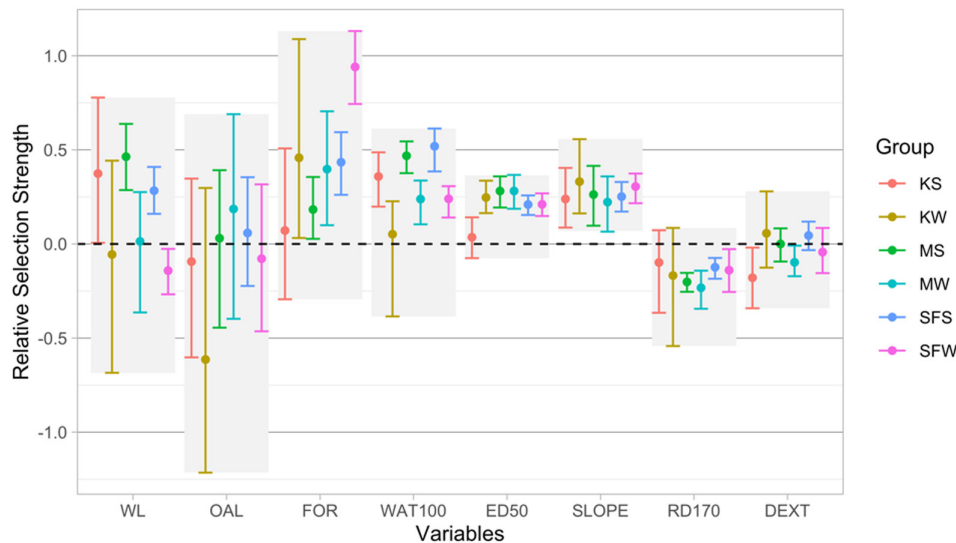
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Figure 2. Relative selection strength for eight landscape features from the combined model with 95% confidence intervals for female cougars with kittens in summer (KS), female cougars with kittens in winter (KW), adult male cougars in summer (MS), adult male cougars in winter (MW), single female cougars in summer (SFS) and single female cougars in winter (SFW) in west-central Alberta, Canada, 2016–2018. Landscape features: WL – shrub and treed wetland, OAL – open agricultural land, FOR – forest, WAT100 – exponential decay of water (100 m), ED50 – exponential decay of edge (50 m), SLOPE – slope, RD170 – exponential decay of road (170 m), DEXT – distance to resource extraction. Beta coefficients and confidence intervals were calculated using inverse variance weighted mean (IVW) from the two-stage resource selection function after bootstrapping 4000 times.

were not significant. Open agricultural land and distance to resource extraction were both variable for all groups.

All significant IVW coefficients from the two-step approach agreed with results of the mixed-effect model (Supplementary material Appendix 1 Table A7), however habitat with 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 to show regions with higher and lower relative selection (Fig. 3). For single females and females with kittens in winter, the west and southwest region of the study area provided the most-selected habitats (Fig. 3; 1b and 2b), while in summer, quality habitat was more widespread (Fig. 3; 1a and 2a). For males, relative selection was similar for both seasons with higher-quality habitat in the west (Fig. 3; 3a and 3b).

LSD results indicated that seasonal differences in habitat selection occurred for each reproductive status. All groups avoided wetlands and proximity to water during winter in comparison to summer (Table 6). Females with kittens and

single females also had greater selection for forested habitat during winter in relation to summer. Females with kittens selected areas further from resource extraction (DEXT) during winter compared to summer, while single females and males selected areas closer to DEXT in winter compared to summer. Furthermore, females with kittens in winter avoided open agricultural lands and selected edge habitat in relation to females with kittens in summer.

During summer, females with kittens selected proximity to water and edge habitat less, and areas closer to resource extraction more than single females and males (Table 7). Females with kittens also selected areas of lower slope than single females. In winter, females with kittens avoided open agricultural areas, proximity to water and areas close to resource extraction than single females and males (Table 8). Females with kittens also avoided areas closer to roads, and selected less sloped terrain than single females and males in winter, respectively.

We found that during summer, single females had greater selection for wetlands and forested habitat and lower selection for areas close to water and resource extraction than

Table 3. Seasonally stratified population level inverse variance weighted (IVW) coefficients for adult male cougars in summer and winter in west-central, Alberta, Canada, 2016–2018. The contribution of each variable to the model is indicated by the rank column. MS=males in summer, MW=males in winter. LCI=lower 95% confidence interval, UCI=upper 95% confidence interval. See Table 1 for acronyms.

Variables	MS				MW			
	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

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Table 4. Seasonally stratified population level inverse variance weighted (IVW) coefficients for single adult female cougars in summer and winter in west-central, Alberta, Canada, 2016–2018. The contribution of each variable to the model is indicated by the rank column. SFS = single females in summer, SFW = single females in winter. LCI = lower 95% confidence interval, UCI = upper 95% confidence interval. See Table 1 for acronyms.

Variables	SFS				SFW			
	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

males (Table 9). During winter, single females had greater selection for forested habitat, areas closer to roads and more sloped terrain than males. Although the magnitude was small, single females had lower selection for areas closer to edge habitat in relation to males.

Discussion

Habitat selection for all cougars was best predicted by the combined model, indicating that no one variable type drove habitat selection. The top model contained variables that could be important for safety and visibility during hunting (SLOPE), related to anthropogenic disturbance (DEXT and RD170) and habitat (WL, OAL, WAT100, ED50 and FOR) and supported our predictions that these variables would be important for each group. A robust variable describing prey availability across the study area and throughout the year may have benefitted our modelling for cougar habitat selection. However, obtaining suitable prey data would have been logistically complicated and required resources beyond those available. We believe habitat features that were selected reflect areas where prey was likely to occur or were more vulnerable to predation.

Common habitat selection patterns

Areas closer to edge habitat were consistently selected for by all groups, 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. 2014). Cougars rely on camouflage and sufficient cover to approach unsuspecting prey to a distance where a 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 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 our 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, the most common prey of cougars in the study area (Knopff et al. 2010), commonly feed in open grassy areas, and in combination with good stalking cover provided by adjacent forests, 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 summer, areas closer to water were among the most important habitat features for all groups of cougars. Similarly, Dickson and Beier (2002) reported cougars in California selected areas closer to riparian areas. Riparian habitat and areas closer to water typically have higher prey density and dense cover and probably provide cougars in west-central Alberta with quality areas to stalk prey (Compton et al. 1988). In California, cougar kill sites were primarily located in creek bottoms and vegetation types associated with prox-

Table 5. Seasonally stratified population level inverse variance weighted (IVW) coefficients for female cougars with kittens in summer and winter in west-central, Alberta, Canada, 2016–2018. The contribution of each variable to the model is indicated by the rank column. KS = females with kittens in summer, KW = females with kittens in winter. LCI = lower 95% confidence interval, UCI = upper 95% confidence interval. See Table 1 for acronyms.

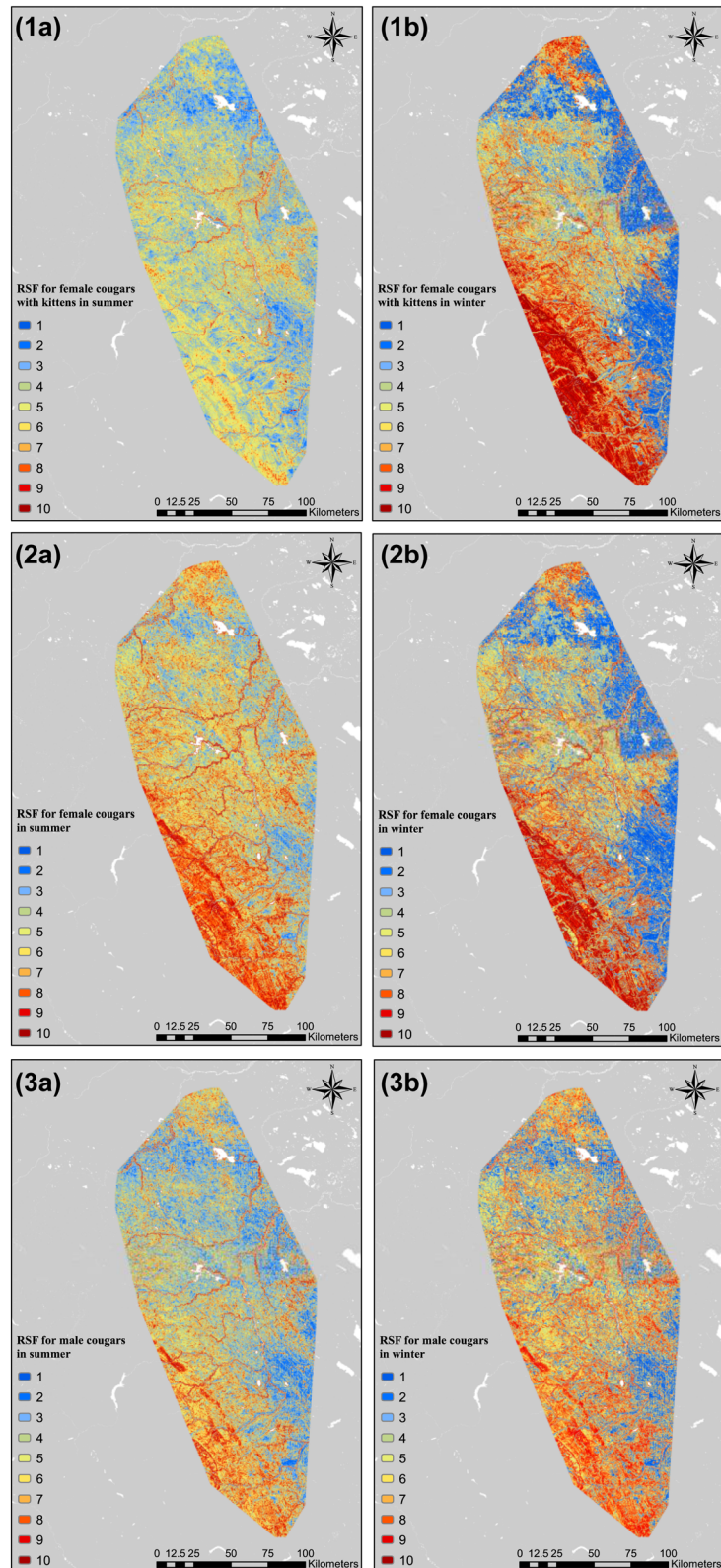| Variables	KS				KW			
	IVW	Rank	LCI	UCI	IVW	Rank	LCI	UCI
WL	0.374	1	0.006	0.778	−0.056	7	−0.685	0.443
OAL	−0.094	6	−0.603	0.347	−0.614	1	−1.215	0.298
FOR	0.071	7	−0.294	0.508	0.458	2	0.032	1.089
WAT100	0.359	2	0.198	0.487	0.052	8	−0.385	0.227
ED50	0.036	8	−0.075	0.142	0.247	4	0.164	0.336
SLOPE	0.239	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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Figure 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 6. Latent selection difference function comparing habitat selection between seasons for each cougar reproductive status in west-central Alberta, Canada. For each group, winter was coded as 1 and summer as 0. Table shows the beta coefficients β, robust standard errors (SE) and statistical significance (p) for each pairing. KW= females with kittens in winter, KS=females with kittens in summer, SFW=single females in winter, SFS=single females in summer, MW=males in winter, MS=males in summer. See Table 1 for acronyms. $p \leq 0.05^*$.

Variables	KW × KS			SFW × SFS			MW × MS		
	β	SE	p	β	SE	p	β	SE	p
WL	−0.509	0.232	0.028*	−0.394	0.188	0.036*	−0.536	0.210	0.011*
OAL	−0.763	0.385	0.047*	−0.010	0.300	0.739	0.160	0.290	0.583
FOR	0.559	0.268	0.027*	0.464	0.229	0.043*	0.249	0.217	0.253
WAT100	−0.491	0.130	<0.001*	−0.239	0.047	<0.001*	−0.263	0.054	<0.001*
ED50	0.254	0.050	<0.001*	−0.022	0.026	0.407	−0.018	0.036	0.612
SLOPE	0.074	0.053	0.164	0.032	0.027	0.235	−0.060	0.033	0.071
RD170	−0.042	0.070	0.552	−0.026	0.035	0.459	−0.068	0.047	0.146
DEXT	0.551	0.069	<0.001*	−0.120	0.024	<0.001*	−0.183	0.031	<0.001*

imity to water (Hopkins 1989, Beier et al. 1995). Areas close to water are likely less important in winter because water is available from snow and most water bodies are frozen.

Severe winter conditions decrease deer survival, resulting in lower densities in 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 spring and early summer. The thawing of 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 hunting beaver, amplifying their selection for this habitat type during summer and is reflected in the telemetry data. Similarly, cougars in Washington State commonly preyed upon beaver and deer along water bodies (Kertson and Marzluff 2011). Cougars also had similar selection patterns for wetlands which was more important for habitat selection during summer 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 habitat were supported. All groups selected forested habitat 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 our study area, cougars are subordinate to bears and wolves. We therefore suggest that forested habitat provides good hunting and escape from bears and wolves for cougars of all sex and reproductive status as they often climb trees to avoid direct conflict.

Similar to other studies (Logan and Irwin 1985, Arundel et al. 2007, Kusler et al. 2017), all cougars selected steeper terrain. 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 winter (Kusler et al. 2017). Steep embankments along 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 (roads with a 170 m buffer radii) was the most important for cougar habitat selection except for females with kittens in summer. All groups avoided proximity to roads, although for females with kittens, selection was not significant. The trend observed in our results supported the prediction that cougars of all reproductive status would avoid roads in both seasons and was similar to past studies (Arundel et al. 2007, Knopff et al. 2014). However, Knopff et al. (2014) reported that cougars used areas closer to roads at night compared

Table 7. Latent selection difference function comparing cougar habitat selection between females with kittens and both single females and males during summer in west-central Alberta, Canada. For each pairing, females with kittens were coded as 1 and single females and males were 0. Table shows the beta coefficients β, robust standard errors (SE) and statistical significance (p) for each pairing. KS=females with kittens in summer, SFS=single females in summer, MS=males in summer. See Table 1 for acronyms. $p \leq 0.05^*$.

Variables	KS × SFS			KS × MS		
	β	SE	p	β	SE	p
WL	0.097	0.207	0.641	−0.054	0.211	0.791
OAL	−0.387	0.305	0.204	−0.341	0.329	0.300
FOR	−0.445	0.252	0.077	−0.131	0.248	0.597
WAT100	−0.360	0.065	<0.001*	−0.231	0.064	<0.001*
ED50	−0.175	0.042	<0.001*	−0.268	0.042	<0.001*
SLOPE	−0.137	0.042	0.001*	−0.054	0.043	0.207
RD170	−0.097	0.051	0.057	−0.005	0.052	0.929
DEXT	−0.255	0.039	<0.001*	−0.337	0.044	<0.001*

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Table 8. Latent selection difference function comparing cougar habitat selection between females with kittens and both single females and males during the winter period in west-central Alberta, Canada. For each pairing, females with kittens were coded as 1 and single females and males as 0. Table shows the beta coefficients β, robust standard errors (SE) and statistical significance (p) for each pairing. KW=females with kittens in winter, SFW=single females in winter, MW=males in winter. See Table 1 for acronyms. p ≤ 0.05*.

Variables	KW × SFW			KW × MW		
	β	SE	p	β	SE	p
WL	0.027	0.200	0.891	−0.100	0.253	0.693
OAL	−1.071	0.348	0.002*	−1.394	0.392	<0.001*
FOR	−0.452	0.239	0.059	0.114	0.273	0.675
WAT100	−0.589	0.089	<0.001*	−0.478	0.100	<0.001*
ED50	0.044	0.039	0.257	−0.011	0.046	0.803
SLOPE	−0.064	0.038	0.088	−0.089	0.045	0.049*
RD170	−0.245	0.057	<0.001*	−0.054	0.066	0.416
DEXT	0.300	0.048	<0.001*	0.301	0.051	<0.001*

to day, and could be related to deer using these areas when vehicle activity is low. Roads can have many ecological effects on biotic communities including noise pollution (Spellerberg 1998). The eastern portion of the study area is highly fragmented and contains a dense network of logging and oilfield roads. Noise pollution can affect an animal's ability to receive acoustic signals (Brumm 2004, Scobie et al. 2014) and may prevent cougars from assessing their surroundings and deterring them from roads.

Seasonal habitat selection differences

Seasonality changes the availability of resources, and depending on the reproductive status of an individual, certain habitat features become more important. Habitat variable ranking and LSD indicated that habitat selection was variable between season for all groups with the importance of some covariates varying by season. For males and especially single females, the ranking of variables in summer were similar to that of winter, with only a few habitat types having a noticeable change in importance. The greatest seasonal difference for males was the high selection for wetlands in summer with forests having a lower rank, which switched to wetlands being the least important habitat and forests being the highest ranked during winter. Similar differences occurred for single females, with wetlands being higher ranked and selected in summer and lower ranked and avoided in winter. The seasonal difference observed in both single adult classes may be due to seasonal changes in prey use of wetlands. Black spruce and tamarack found in wetlands likely provides little browse for deer during win-

ter, and the low prey density in these areas likely presents few hunting opportunities for cougars. Overall, males and single females had similarly ranked habitat in both seasons. Although behavioral differences occur between males and single females, the most important habitat for each likely reflects regions with quality hunting opportunity.

Season affected the importance of multiple habitat features for females with kittens. Proximity to water and wetlands were selected and the most important features for females with kittens in summer and similar to males and single females, wetlands were less important during winter. However, proximity to water remained important for males and single females, but was the lowest ranked habitat feature for females with kittens during winter. Unlike for males and single females, travel corridors along streams and rivers may be less important to females when restricted by offspring mobility. Furthermore, forest and edge habitat were low ranked for females with kittens during summer, but were selected and among the most important in winter. The switching of selected and high ranking habitat from wetland and proximity to water in summer, to edge habitat and forest in winter, may indicate that females were selecting habitat seasonally that provided the best hunting. While open agricultural land had little importance for females with kittens in summer, as was the case for males and single females in both seasons, it was the highest ranked in winter. Retreating to the safety of a tree is a common escape response of cougars when threatened (Logan and Sweanor 2009). For cougar kittens, the lack of trees and potential of deep snow on agricultural land could make escaping predators difficult and provide little refuge from the harsh winter environment

Table 9. Latent selection difference function comparing cougar habitat selection between single females and males during both the summer and winter period in west-central Alberta, Canada. For each pairing, single females were coded as 1 and males as 0. Table shows the beta coefficients β, robust standard errors (SE) and statistical significance (p) for each pairing. SFS=single females in summer, MS=males in summer, SFW=single females in winter, MW=males in winter. See Table 1 for acronyms. p ≤ 0.05*.

Variables	SFS × MS			SFW × MW		
	β	SE	p	β	SE	p
WL	0.394	0.188	0.036*	−0.079	0.237	0.740
OAL	−0.100	0.300	0.739	−0.186	0.357	0.602
FOR	0.464	0.229	0.043*	0.565	0.265	0.033*
WAT100	−0.239	0.047	<0.001*	0.091	0.058	0.115
ED50	−0.022	0.026	0.407	−0.080	0.037	0.032*
SLOPE	0.032	0.027	0.235	0.151	0.036	<0.001*
RD170	−0.026	0.035	0.459	0.138	0.052	0.008*
DEXT	0.300	0.024	<0.001*	0.029	0.041	0.486

of western Alberta. For such reasons, females with kittens may avoid open agricultural land during winter and select habitat that will provide safety for offspring.

Habitat selection of females with kittens compared to single females and males

There were notable differences in rank and sign of selection for females with kittens compared to the other groups. In addition to open agricultural land for females with kittens in winter, areas close to active well-sites and compressor stations were medium ranked for females with kittens in both seasons and significantly selected during summer, while being low in importance for males and single females throughout the year. In Alberta, well-pads and compressor stations are surrounded by a hectare of cleared land that is usually revegetated with agronomic species that attracts white-tailed deer (Dawe et al. 2014, Lupardus et al. 2019). A small area with abundant forage could hold high densities of deer and provide females with kittens with frequent hunting opportunity.

Individual variation was the greatest for females with kittens in both seasons as indicated by the large IVW confidence intervals (Fig. 2) and may indicate high behavioral differences of females with offspring. Furthermore, as kittens become older, they require less parental care and by four months old are weaned and capable of climbing trees to escape predators (Logan and Sweanor 2009). Kitten age may influence 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 and limited statistical power.

Habitat selection across the study area

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 was especially true for females with and without kittens in winter (Fig. 3). The eastern portion of the study area is dominated by 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, forested landscapes are less fragmented further west and may provide thermoregulatory advantages for both prey (Parker and Gillingham 1990) and females with kittens (Kusler et al. 2017). During 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 when ground vegetation and deciduous tree foliage regrows, providing more forage for prey and cover for cougars.

Overall, cougars consistently selected for edge habitat, proximity to water and forested areas, while avoiding proximity to roads. Seasonally, habitat features appeared to vary in importance for cougars of different sex and reproductive status, and was most evident for females with kittens. Among the three reproductive statuses, females with kittens appear to differ the most in habitat selection compared to males and single females. Our results provide insight on cougar ecology at northern latitudes with information on important variables of habitat selection.

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Supplementary material (available online as Appendix wlb-00735 at <www.wildlifebiology.org/appendix/wlb-00735>). Appendix 1.