YUKON MOOSE: I. SEASONAL RESOURCE SELECTION BY MALES AND FEMALES IN A MULTI-PREDATOR BOREAL ECOSYSTEM

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ABSTRACT: Moose (*Alces alces*) in Yukon experience an extreme range of thermal conditions, highly variable snow depths, natural and anthropogenic disturbances, predation by wolves and grizzly bears, and hunting pressure. Our objective was to identify variables that best explained habitat-selection patterns of moose in south-central Yukon for use in land-use planning and impact assessment. We evaluated selection of land-cover class, elevation, aspect, predation risk, and harvest vulnerability using resource selection functions. We created pooled models for males and females by averaging models for individuals by sex and season. Selection of shrub-dominated land cover highlighted the importance of forage accessibility throughout the year. Selection for elevation, aspect, and cover changed throughout the year, as influenced by climatic conditions. By selecting mixed cover types during calving and summer, female moose presumably balanced needs for both cover and forage. Males minimized harvest vulnerability during rut. Moose, in general, demonstrated highly variable habitat selection; however, consistent individual responses between sexes supported trends identified by pooled selection coefficients, as well as detected trends among males and females. The greatest amount of individual variation occurred during the growing season and the least amount during late winter, suggesting that climatic factors limited the options available to moose at a critical time of the year.

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Habitat selection is a hierarchical process in which an animal first chooses a general place in which to live (a habitat or habitats) and then makes subsequent decisions about how it moves within the habitats and responds to environmental factors (Anderson et al. 2005). Many factors, even those beyond the extent of the home range, influence how animals respond to their environment (Kie et al. 2002, Bowyer and Kie 2006). Effective wildlife management benefits from understanding seasonal selection patterns and how animals respond to key habitat variables resulting in those patterns.

Moose (*Alces alces*) use a wide variety of habitats in various successional stages throughout the boreal forest (Kelsall et al. 1977). As with most large herbivores, habitat selection is driven by the need to meet nutritional requirements with adequate forage and cover, and to minimize mortality risk. Moose feed on a wide variety of plant species (Miquelle and Jordan 1979), and require large amounts of forage because of their large body size (Renecker and Hudson 1992, Renecker and Schwartz 2007). They adjust foraging behaviour in response to seasonal changes in forage quality and quantity (Andersen and Saether 1992). Habitat selection by moose is strongly influenced by ambient conditions: both vegetative cover and topography affect microclimate, snow depth and density, and predation risk (Mysterud and Ostbye 1999). Moose use cover and topography in all seasons to moderate extremes of cold (<-30 °C in winter) and heat stress (Renecker and Hudson 1986), and increase use of cover with increasing snow depth, density, or crusting (Telfer 1970, Van Ballenberghe and Peek 1971). Wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and black bears (*Ursus americanus*) are the primary predators of moose in boreal systems, and deep snow may impair defensive capabilities of moose against wolves (Peterson and Allen 1974). The vulnerability of moose to predation is also influenced by their age, size, and body condition, population densities of both moose and predators, and the availability of alternative prey (Hayes et al. 2000). Anti-predator behaviour varies with the degree of predation risk, group size, experience, and sex. Moose behaviour and population dynamics are further affected by moose density, which itself is influenced by hunter density, timing of the hunting season, and accessibility (Baskin et al. 2004).

In addition to the effects of seasonal changes in forage, climate, and risk, differences in body size and reproductive roles between male and female moose can further modify habitat selection. Sexual segregation, as the differential use of space by the sexes outside of the breeding season, is widespread in sexually dimorphic ungulates such as moose. Most hypotheses for sexual segregation relate to reproductive strategies, sexual dimorphism, and/or social factors (Main et al. 1996). These hypotheses suggest that males should maximize body condition before rut and minimize energy expenditures during winter, even if predation risk increases. Larger rumen size allows males to target large quantities of coarse forage and larger body size puts them at less risk of predation. In contrast, females have smaller digestive capacity, greater energetic demands of gestation, parturition and lactation, and potentially higher exposure to predation risk. Females should feed more frequently while targeting areas with higher-quality forage in close proximity to cover (Barboza and Bowyer 2000) to meet minimum resource requirements while maximizing security of calves (Main and Coblentz 1990).

Relatively few studies have addressed habitat requirements and limiting factors of moose in Yukon, where the distribution of moose reaches some of the most northern limits of the species' range. Moose in Yukon experience extreme thermal conditions, highly variable snow depths, natural and anthropogenic disturbances that alter land cover, predation by wolves and grizzly bears, and hunting pressure (Kelsall and Telfer 1974). Moose are a focal species of many northern communities for subsistence, cultural, economic and recreational values (Timmerman and Rodgers 2005).

The overall objective of this study was to identify variables that best explained seasonal resource selection patterns of moose in south-central Yukon for subsequent use in land-use planning and impact assessment. Prior to our study, relatively little was known about the distribution, abundance, or habitat use of Yukon moose outside of the early winter, post-rut period (Larsen et al. 1989, Gasaway et al. 1992, Florkiewicz and Henry 1994, Boertje et al. 1995, Keith 1995, Mauer 1998, Hayes and Harestad 2000, Hayes et al. 2000). We incorporated topographical attributes, land cover, predation risk from wolves and grizzly bears, and harvest vulnerability into resource selection models. Resource selection functions (RSF) describe the relative selection of attributes used by an animal (Manly et al. 2002) and provide a broad-scale perspective of general selection patterns on the landscape (Boyce and McDonald 1999). They help define which attributes have the greatest influence on habitat use and how selection of different attributes can change among seasons. We hypothesized that moose would optimize survival by selecting landcover classes that minimize energy losses in winter and maximize potential forage intake during the growing season. Because of physiological and reproductive differences, we predicted that male and female moose would use different selection patterns to meet these needs. In addition to metabolic demands, moose also faced exposure to mortality risk from predators and hunters. We predicted that females would reduce exposure to predation risk throughout the year, particularly when calves were young, and that males would reduce exposure to harvest risk during the hunting season.

STUDY AREA

The South Canol study area in south-central Yukon was 130 km east of Whitehorse and 100 km north of Teslin, between 60.4743 and 61.9082° N latitude, and 128.9699 and 135.2570° W longitude. Covering approximately 35,000 km^2, it extended north from Johnson's Crossing, east of Lake Laberge, west of Frances Lake, and south of the community of Ross River (Fig. 1). Climate in the South Canol area was characterised by short cool summers and long cold winters. Mean annual precipitation ranged from 500–650 mm with most as snow in winter. Mean annual temperature was -3 °C, with a mean January temperature of -20 °C and a mean July temperature of 10 °C (Yukon Ecoregions Working Group 2004). Unlike many other areas of the Yukon, the South Canol area had few wildfires in the past 60 years (Yukon Department of Energy, Mines and Resources 2004). The area was in the Boreal Cordillera Ecozone and includes the Pelly Mountains Ecoregion with small portions of the Southern Lakes Ecoregion. The Pelly Mountain Ecoregion is a rolling plateau topped by numerous mountain peaks and dissected by small rivers. The Southern Lakes Ecoregion is characterized by dissected plateaus, rolling hills, and broad

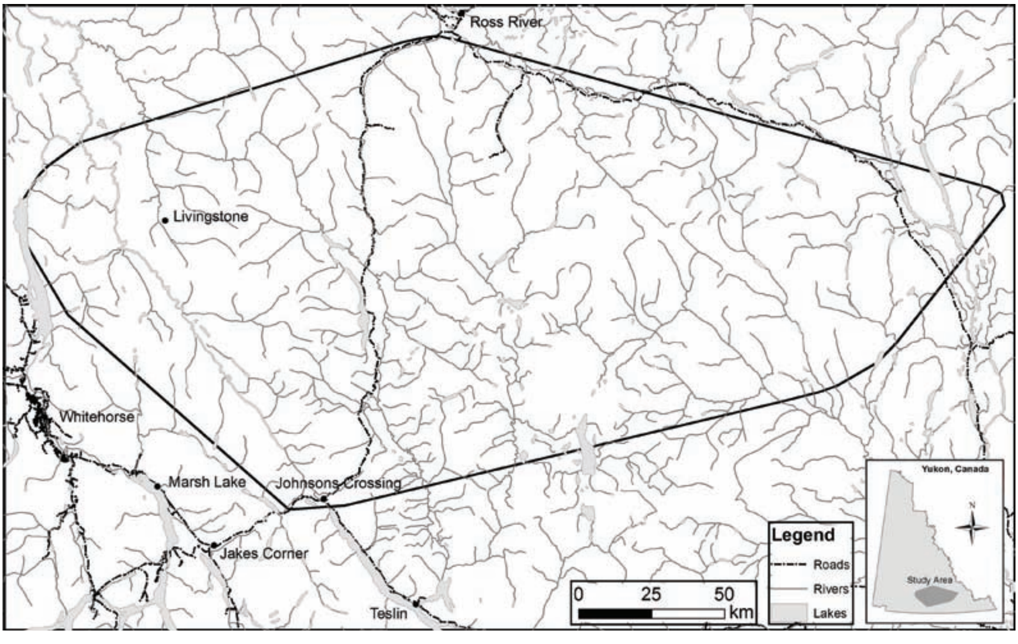

Fig. 1. South Canol moose study area located in south-central Yukon, Canada.

valleys occupied by lakes and rivers (Yukon Ecoregions Working Group 2004). The entire area is within the sporadic discontinuous permafrost zone. Shrub and dwarf shrub tundra vegetation occurred above 1,350 m above sea level (a.s.l.), and coniferous and mixed forests occurred below 1,350 m a.s.l.

In 2007, the average population density was 241 moose/1000 km^2 within a 6,735-km^2 core portion of the study area, a density 1/3 higher than the Yukon average of 158 moose/1000 km^2 (Florkiewicz et al. 2008). There were approximately 22 calves, 18 yearlings, and 76 males for every 100 adult female moose. The area also encompassed the ranges of 5 woodland caribou (*Rangifer tarandus*) herds, including the Wolf Lake, Pelly, Carcross, Atlin, and Laberge herds (Yukon Ecoregions Working Group 2004). Stone's sheep (*Ovis dalli stonei*) used the Big Salmon Range in the northern part of the study area, and wolves, grizzly bears, and black bears occurred throughout the area. Wolf density was estimated as 8–12 wolves/1,000 km^2 (R. Ward, Yukon Department of Environment, pers. comm., Baer 2011), and the grizzly bear estimate was 15.2 bears/1000 km^2 (R. Florkiewicz, Yukon Department of Environment, pers. comm.). Black bear density was unknown, but assumed lower than grizzly bears and with less predatory impact than either wolves or grizzly bears.

The South Canol area falls mainly within the traditional territory of the Teslin Tlingit First Nation and also includes portions of the Ta'an Kwäch'än, Kwanlin Dun, and Kaska traditional territories. Eight Game Management Subzones (GMS), one big-game outfitting concession, and portions of 17 registered trapping concessions were in the study area. Approximately half of the trapping concessions were operated by local First Nations (T. Boyes, Teslin Tlingit Council, pers. comm.). The average annual reported moose harvest (2002–2006) in the area was approximately 1.7% of the population (Florkiewicz et al. 2008). This estimate did not include unreported First Nations harvest which was estimated to equal the licensed harvest.

Very little development was present in the study area. The South Canol Road, as a seasonal unpaved highway that extends from Johnson's Crossing to Ross River, provided access through the eastern portion of the study area (Fig. 1). The Pelly Mountains Ecoregion is considered rich in mineral deposits (Yukon Ecoregions Working Group 2004), but only one hard-rock mineral claim (Tintina Mines Ltd.) was active during our study. An exploration road was upgraded in 2008 and extended 76 km from the South Canol Road to Red (Slate) Mountain within the study area. This exploration road was accessible by ATV and 4x4 vehicle in summer and by snowmobile in winter. Several small placer-mining operations, some with airstrips and limited roads, were present in the remote northwest portion of the study area.

METHODS

Animal captures and telemetry data

Twenty-seven moose (9 males, 18 females) were captured between 26 February and 27 March 2008 and fitted with global positioning satellite (GPS) collars (15 collars: Lotek GPS4400M ARG, New Market, Ontario, Canada; 12 collars: Habit Research Inc., Victoria, British Columbia, Canada). The GPS collars were programmed to acquire locations 6–8 times per day over a 24-h cycle and periodically uploaded data to the ARGOS satellite. Location data were downloaded from ARGOS once per month. We used Spatial Viewer (M. Gillingham, unpublished Visual Basic program) to examine movement patterns of individual animals and to identify and eliminate errant location points (i.e., those points that were an improbable distance from previous points) that were likely the result of GPS errors. Fifteen collars provided 2 complete years of location data, and 9 collars transmitted for at least one full season. Three collars transmitted for less than one season and these were not used in analyses. We retrieved 77,309 valid locations from the 24 collars (8 males and 16 females for our selection analyses) with average fix rates of 88 ± 4% ($\bar{x}$ ± SE) for males and 66 ± 7% for females.

We defined 5 seasons based on moose life-history and habitat characteristics: Calving (15 May–30 Jun), Summer (1 Jul–14 Aug), Rut (15 Aug–31 Oct), Early Winter (1 Nov–28 Feb), and Late Winter (1 Mar–14 May). These dates generally corresponded with the timing of seasons in other moose studies in Yukon, Alaska, and British Columbia (Larson et al. 1989, Miquelle et al. 1992, Gillingham and Parker 2008a, b). In our analyses we considered 4 groups of individual moose based on sex and reproductive status: we compared males to females, and females without calves to females with calves. Calf status of females was based on aerial surveys during mid-June, October–November, and March from June 2008 through March 2010. Only females of known calf status were used in analyses. For example, if a moose had a calf in June and then again in November (i.e., Calving and Early Winter), we also assumed the calf was present during Summer and Rut. If she was alone in November, however, then she was classified as unknown calf status during Summer and Rut, and with no calf during Early Winter. We conducted similar analyses for each of the 4 groups of moose, including male moose during the Calving period, to compare selection patterns between sexes at this time of year when the onset of greening occurred.

Study design

We used resource selection functions (RSFs) to assess habitat selection of moose in the South Canol study area. Coefficients were estimated using logistic regression software (Stata version 12, StataCorp 2011) for the parameters of exponential RSFs with used and available points for individual animals (Design 3: Thomas and Taylor 1990, 2006). Used points were the GPS fixes from each radio-collared moose. Availability was identified by selecting 5 random points from within a buffer surrounding each location point. The radius of each buffer was based on the 95th percentile movement distance of each individual in each season. We assumed the individual could have potentially moved anywhere within this buffer over the period represented by the GPS fix. We then used raster remote-sensing software to query the attributes of each used and available point.

Attributes for resource selection

Land-cover composition.-- We developed a land-cover classification using Earth Observation for Sustainable Development of Forests (EOSD) land-cover information, a digital elevation model (DEM), and National Topographic Data Base (NTDB) hydrology information (www.geomaticsyukon.ca). EOSD (circa 2002) was interpreted from Landsat-7 imagery with 25-m resolution and was used to classify land-surface elements (e.g., vegetation, water, rock) (Wulder et al. 2003). Using remote-sensing software (Geomatica 10.3, PCI Geomatics 2009), we combined 26 EOSD cover classes with the above-mentioned data sources to produce 8 land-cover classes relevant to moose ecology (Table 1). Classes were combined based on similarities in vegetation and elevation. Grouping classes also had the effect of improving the accuracy of EOSD data, which approached 75–80% (M. Waterreus, Yukon Department of Environment, pers. comm.).

Topographic variables.-- Elevation and aspect were extracted from a DEM using ArcMap (ArcMap 9.3, ESRI 2006). We entered elevation as a quadratic in all selection models

Table 1. Description of 8 land-cover classes used by radio-collared moose in the South Canol study area of south-central Yukon, Canada.

Land-cover Class	Description
Conifer	Spruce, pine, or subalpine fir covering 75% or more of total basal area.
Mixed Wood	A mix of conifers or deciduous trees with neither exceeding 75% of total basal area.
Lowland Shrub	Areas below 1,300 m a.s.l. with ≥ 20% vegetative cover of which at least 33% is shrub species. Also includes deciduous trees exceeding 75% of total basal area.
Upland Shrub	Areas above 1,300 m a.s.l. with ≥ 20% vegetative cover of which at least 33% is shrub species. Also includes deciduous trees exceeding 75% of total basal area.
Alpine	Areas above 1,300 m a.s.l with ≥ 20% vegetative cover. Includes snow, ice, exposed land, and areas with no data above 1,300 m a.s.l. Excludes Upland Shrub.
Lowland Open	Areas below 1,300 m a.s.l with ≥ 20% vegetative cover, or exposed land with < 5% vegetation. Excludes Lowland Shrub.
Water	Lakes, ponds, reservoirs, rivers, streams, or creeks.
Riparian	Areas within 25 m of small (1-line[1]) water courses; areas within 100 m of larger water courses (2-line) and water bodies. Includes wetlands.

[1] 1-line streams are smaller streams indicated on 1:50,000 maps with a single line, whereas 2-line streams are indicated using 2 lines to delineate the shores of large rivers.

to be able to discriminate selection for mid-elevation locations. To reduce the number of categorical variables, we converted aspect into 2 continuous variables: northness and eastness (Gillingham and Parker 2008a, b). Northness (the cosine of aspect) values range from 1.00 to -1.00, indicating north through south aspects. Eastness (the sine of aspect) values range from 1.00 to -1.00, indicating east through west aspects. The values for both northness and eastness must be interpreted together to understand selection for aspect. For example, values near zero for both northness and eastness indicate no selection for aspect, whereas large negative values for both northness and eastness indicate selection for southwest aspects. Slopes of ≤ 1° were not assigned an aspect.

Predation risk.--Predation risk to moose was defined using RSFs developed for data from GPS-collared wolves and grizzly bears in the Besa-Prophet area of northern British Columbia (Milakovic 2008; Milakovic et al. 2011, 2012). These predator-selection models included elevation, slope, aspect, vegetation type, and fragmentation (an index of vegetation diversity). We assumed that risk of predation to moose by wolves and grizzly bears was directly related to selection values for the predators. We generated predation-risk surfaces for moose in the South Canol area as GIS raster layers that defined selection value to wolves or grizzly bears in each season by applying the coefficients from the Besa-Prophet predator-selection models to each 25 x 25-m pixel, based on its topographic and land-cover features. We scaled values from zero to 1 to standardize selection surfaces and to facilitate comparison between seasons. We created 5 seasonal wolf risk surfaces, and 3 seasonal grizzly bear risk surfaces (with no risk during hibernation seasons).

In addition to predation risk as a variable in resource selection models, we calculated the average predation risk that each individual moose was exposed to in each season (based on predation-risk values predicted from the predation-selection models (as above) at GPS locations). We set a minimum of 100 location points per individual in each season to be included in calculations. We used a repeated measures 2-way analysis of variance (ANOVA) to investigate whether these predation-risk values differed between sexes and among seasons. Post-hoc analyses for significant ($\alpha = 0.05$) effects were assessed using Bonferroni-corrected confidence intervals on marginal means (Margins in Stata version 12, StataCorp 2011). We used 1-way ANOVAs to determine if the average predation risk incurred by females with and without calves differed in each season.

Harvest vulnerability.--Harvest information was collected from 63 First Nations and licensed resident hunters who harvested moose in the study area during the 5 years before moose telemetry locations (i.e., 2004–2008). We collected information about the characteristics of sites where moose were killed. Interviewees were asked to specify on a map where the kill occurred, to comment on proximity to road or water access, and to identify which land-cover class the animal was in, based on examination of several representative photographs of the different land-cover classes (McCulley 2015).

We developed a raster surface that defined harvest vulnerability to male moose during Rut using the location data collected from 63 hunters, land-cover classes, and NTDB hydrology and road information. This surface was based on a matrix that included each land-cover class, in combination with distance to both roads and large rivers (> 500 m or < 500 m from each). The number of moose killed, as recorded in the interviews, was entered into each cell of the matrix. Ninety-nine kills were documented in 13 cover-access combinations, with over 80% occurring in the Riparian, Wetland, or Water land-cover classes. To keep harvest vulnerability as a continuous variable, we converted these values into a proportion of the total kills (n = 99). We then assigned the appropriate proportion to each 25 x 25-m pixel based on land-cover class and distance to access.

As with predation risk, we calculated the average harvest vulnerability that each individual was exposed to during Rut. Only individual moose with a minimum of 100 location points were included in calculations. We used a 1-way non-parametric ANOVA (Kruskal-Wallis test because data could not be normalized) to investigate whether average vulnerability to harvest differed ($\alpha = 0.05$) between males and females.

Modeling procedures

We used an information-theoretic approach to evaluate seasonal resource selection by moose (Burnham and Anderson 2002). First, we developed a set of 10 *a priori*, ecologically plausible models to describe resource selection (Table 2). We evaluated the importance of land-cover class, elevation, aspect, predation risk, and harvest vulnerability in the models using selection coefficients (β_i) from logistic regression. A set of 6 models was tested on location data from all moose; we ran 4 additional models for male moose during Rut. We used statistical software for all modeling procedures (Stata version 12, StataCorp 2011). Deviation coding (using DESMAT add-in) was used for all categorical variables. To avoid issues of separation, we dropped both used and available points in land-cover classes where there were ≤ 4 used or available points (Menard 2002). Consequently, very strong avoidance of a particular land-cover class may not always be reflected in the final RSFs. We ranked the model sets using Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002) for small sample sizes. Akaike's weights (w_i) indicate the relative weight of evidence for the top model being the best among the candidate models. We selected a model as the

Table 2. Candidate resource selection models for moose in the South Canol study area, Yukon, Canada. M = males, F = females, L = land-cover class, E = elevation, A = aspect, P = predation risk[1], H = harvest vulnerability.

Model	Late Winter		Calving		Summer		Rut		Early Winter	
	M	F	M	F	M	F	M	F	M	F
L	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
$E + E^2 + A$	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
P	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
$L + E + E^2 + A$	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
$L + E + E^2 + A + P$	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
L + P	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
H							✓			
L + H							✓			
L + P + H							✓			
$L + E + E^2 + A + P + H$							✓			

[1]Both wolf and grizzly bear predation risk during Calving, Summer and Rut; only wolf risk during Early and Late Winter.

likely top model if $w_i \geq 0.95$. We used k-fold cross-validation averaged across 5 random subsets and an averaged Spearman's rank correlation (r_s) to determine the predictive ability of each top model; values of $r_s > 0.70$ indicated good model performance (Boyce et al. 2002). If the top model for each animal had a $w_i < 0.95$, we averaged the selection coefficients (β_i) from the set of top candidate models for which the sum of their respective w_i's was ≥ 0.95 (Burnham and Anderson 2002). When model averaging was required, averaged coefficients from each component model were weighted by their corresponding w_i values; we used a selection coefficient of zero for any parameters not included in an individual's final model to avoid overemphasizing the importance of coefficients that were only in some individual models. Our estimates of pooled variance and standard errors (SE) were based on differences between the coefficient for each model being averaged and the average coefficient across models (weighted by w_i when averaging within competing models for an individual and weighted equally when averaging across individuals; e.g., Murtaugh 2007). Because each individual has a variance associated with its estimate, however, we also included (in an additive manner) the variance of each coefficient in each model in our calculations.

Once we had a single model for each individual, we produced a pooled RSF for males and for females by averaging models across all individuals in that group (using either the top model or an averaged model for each individual as described above) by season. Each model in a sex-season set was equally weighted to avoid over-representation of any individual moose. Models also were developed for females with and without a calf to determine if calf presence affected habitat selection during Calving – a time when newborn calves are most vulnerable.

RESULTS

Seasonal mortality risk

Average exposure to wolf risk was lowest during Early Winter for both male and female moose (Fig. 2A). It was highest during Rut for females and Late Winter for males. Average exposure to grizzly bear

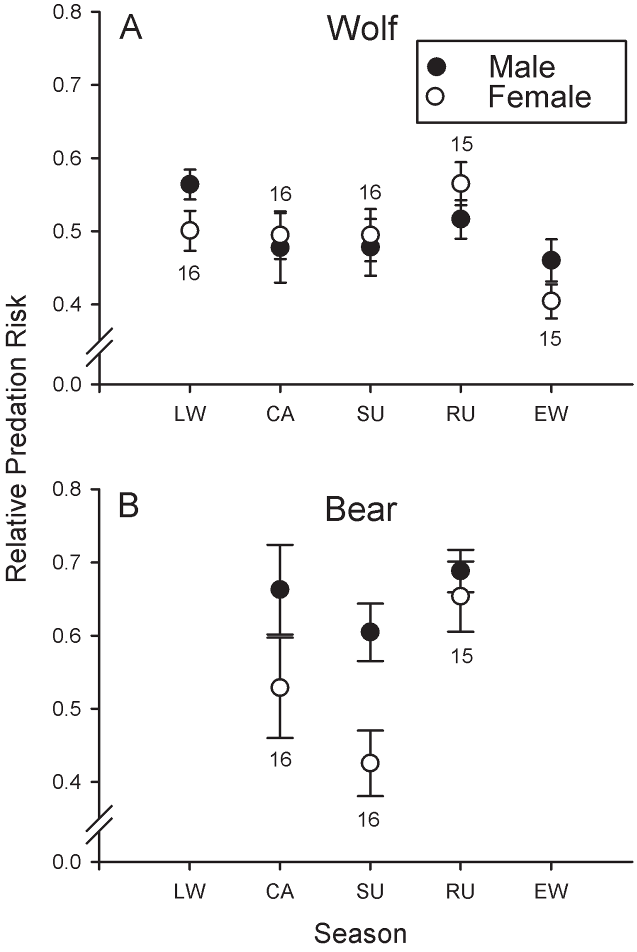

Fig. 2. Average (x̅ ± SE) seasonal predation risk by A) wolves and B) grizzly bears to male (n = 8) and female radio-collared moose in the South Canol area of south-central Yukon, Canada. LW = Late Winter, CA = Calving, SU = Summer, RU = Rut, EW = Early Winter. Numbers indicate sample size of females.

risk was lowest during Summer and highest during Rut for both sexes (Fig. 2B); differences between males and females were not significant (wolves: $F_{1, 88} = 0.07$, $P = 0.79$; bears: $F_{1, 44} = 0.26$, $P = 0.61$). Predation risk was a function of season (wolves: $F_{4, 88} = 5.51$, $P < 0.01$; bears: $F_{2, 44} = 12.08$, $P < 0.01$); wolf risk during Early Winter was lower than during Summer. Calf presence had a significant effect on the wolf risk encountered by females only during Late Winter ($F_{1, 17} = 6.95$, $P = 0.02$), when females with calves used areas with lower risk than females without calves (Fig. 3A). In spring, females with calves used areas with high bear risk (Fig. 3B), although this was not statistically different from the females without calves ($F_{1, 20} = 3.52$, $P = 0.08$). There also was no difference between male and female moose in exposure to harvest risk during Rut (Kruskal-Wallis: $\chi^2 = 0.91$, df = 1, $P = 0.34$).

Seasonal habitat selection

The Late Winter models were represented by the fewest moose (5 males, 7 females), and the Calving models were based

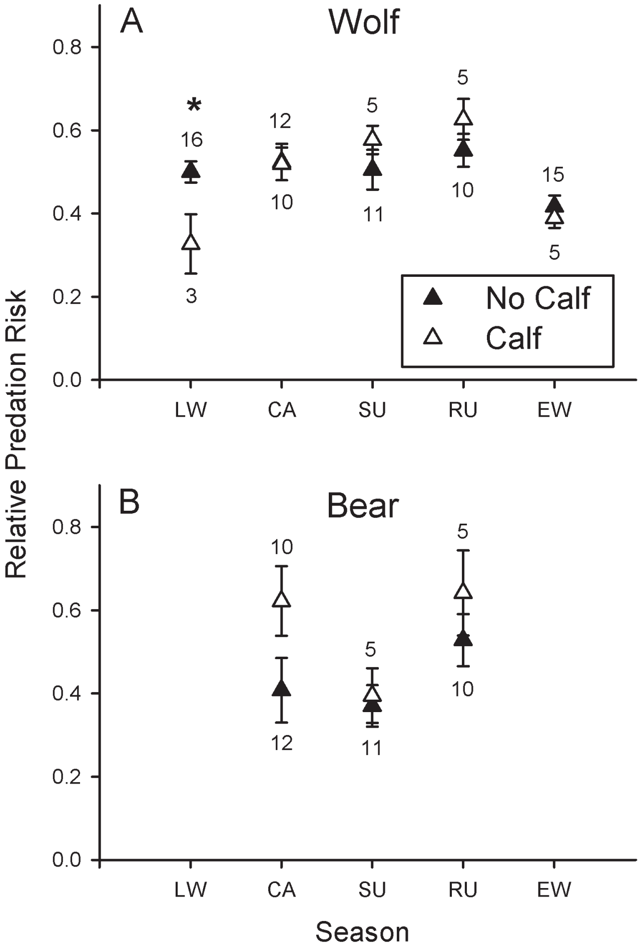

Fig. 3. Average ($\bar{x} \pm$ SE) seasonal predation risk by A) wolves and B) grizzly bears to female radio-collared moose with and without calves in the South Canol area of south-central Yukon, Canada. LW = Late Winter, CA = Calving, SU = Summer, RU = Rut, EW = Early Winter. Numbers indicate sample size. * indicates significant difference.

on the most moose (8 males, 13 females). Each seasonal pooled model included elevation, aspect, predation risk, and all 8 land-cover classes; however, both the sign (+/-) and significance of the coefficients varied seasonally (Tables 3, 4).

Based on the seasonal pooled models, male moose selected for mid-elevations in all seasons (as indicated by positive β_i for elevation and negative β_i for elevation^2). Females had similar selection patterns except during Calving and Summer when elevation was not a significant factor and most variation occurred among individuals. Males selected for west aspects (i.e., significant negative eastness and insignificant northness) during Calving and Early Winter (Table 3), and for southeast aspects (i.e., significant positive eastness and negative northness) in Late Winter as did females. Females selected for west aspects during the Rut and northwest aspects in Early Winter. Relative to predation risk, both sexes selected habitats that had significant grizzly

Table 3. Selection coefficients (Coef ± SE) in pooled resource selection models for male moose, calculated by season for 8 GPS-collared males from 2008–2010 in the South Canol area of south-central Yukon, Canada. As an indication of variability among individuals, the number of individuals that significantly selected for or against each parameter is shown under ++ or - -, respectively. Individuals with insignificant parameters in the model are shown under + and -; n/a refers to number of animals without a parameter. Significant coefficients are in bold.

Season	Late Winter							Calving							Summer						
Model	$E^1 + A^1 + P^1 + L^1$							E + A + P + L							E + A + P + L						
	Coef	SE	+ +	+	-	- -	n/a	Coef	SE	+ +	+	-	- -	n/a	Coef	SE	+ +	+	-	- -	n/a
Elevation (km)	**10.87**	2.10	2	0	0	3	0	**6.62**	1.49	4	1	1	2	0	**20.20**	2.20	5	0	1	1	0
Elevation^2 (km)	**-6.23**	1.00	1	2	0	2	0	**-4.29**	0.71	1	1	1	5	0	**-9.95**	1.01	1	0	1	5	0
Eastness	**0.07**	0.02	2	0	1	2	0	**-0.23**	0.03	1	1	1	5	0	0.00	0.03	3	0	0	4	0
Northness	**-0.28**	0.02	0	1	0	4	0	-0.03	0.04	1	1	3	3	0	0.03	0.02	4	1	1	1	0
Wolf Risk	**0.20**	0.04	3	0	0	2	0	0.01	0.07	2	1	2	3	0	0.00	0.05	2	1	1	3	0
Bear Risk								**1.24**	0.13	7	0	1	0	0	0.05	0.04	3	1	2	1	0
Harvest risk																					
Conifer	**-0.46**	0.03	0	0	0	5	0	**-0.61**	0.05	0	0	1	7	0	**-0.47**	0.03	0	0	3	4	0
Alpine	**-0.15**	0.04	1	0	0	1	3	**-0.07**	0.04	0	0	2	0	6	0.05	0.05	2	2	0	1	2
Lowland Shrub	**0.08**	0.03	2	1	0	2	0	**0.44**	0.05	5	2	0	1	0	-0.05	0.05	2	2	0	3	0
Upland Shrub	**0.16**	0.04	3	0	0	1	1	**0.70**	0.12	4	2	1	1	0	**0.72**	0.05	6	0	0	0	1
Mixed Wood	-0.03	0.05	2	2	0	1	0	**-0.19**	0.06	1	1	2	4	0	**-0.40**	0.04	0	1	0	6	0
Riparian	**0.53**	0.04	4	1	0	0	0	**0.17**	0.06	3	2	1	2	0	**0.13**	0.05	3	1	1	2	0
Water	**0.08**	0.03	1	0	1	0	3	**-0.71**	0.13	0	1	1	2	4	0.03	0.02	1	0	0	1	5
Lowland Open	**-0.21**	0.06	1	0	0	2	2	**0.27**	0.09	1	4	0	1	2	-0.02	0.03	1	1	0	1	4
constant	**-5.99**	1.11	1	1	0	3	0	**-4.51**	0.75	1	1	1	5	0	**-11.56**	1.19	1	1	1	4	0

[1] E = elevation, A = aspect (eastness and northness), P = predation risk (wolf and grizzly bear), L = land-cover class, H = harvest vulnerability.

Table 3 continued....

Table 3. continued

Season	Rut							Early Winter						
Model	E + A + P + L + H							E + A + P + L						
	Coef	SE	+ +	+	-	- -	n/a	Coef	SE	+ +	+	-	- -	n/a
Elevation (km)	**10.20**	1.09	7	0	0	1	0	**19.74**	1.34	6	1	0	0	0
Elevation^2 (km)	**-4.66**	0.42	1	0	0	7	0	**-8.66**	0.56	0	0	0	7	0
Eastness	0.01	0.02	5	0	1	2	0	**-0.09**	0.01	1	1	0	5	0
Northness	**0.25**	0.02	7	0	0	1	0	0.03	0.01	4	0	0	3	0
Wolf Risk	**-0.07**	0.03	3	0	1	4	0	0.04	0.02	2	2	1	2	0
Bear Risk	0.09	0.05	4	0	1	3	0							
Harvest risk	**-6.47**	0.86	2	0	0	4	2							
Conifer	**-0.59**	0.02	0	0	0	8	0	**-0.78**	0.03	0	0	0	7	0
Alpine	**-0.32**	0.05	1	0	2	5	0	**-0.51**	0.05	0	1	0	5	1
Lowland Shrub	0.00	0.03	4	0	1	3	0	**0.16**	0.02	5	1	1	0	0
Upland Shrub	**0.97**	0.03	8	0	0	0	0	**0.34**	0.03	5	0	0	1	1
Mixed Wood	**-0.36**	0.02	0	0	1	7	0	**-0.50**	0.04	0	0	2	5	0
Riparian	**0.48**	0.03	7	0	1	0	0	**0.95**	0.03	7	0	0	0	0
Water	**-0.29**	0.04	0	0	1	3	4	**0.43**	0.10	2	0	1	2	2
Lowland Open	**0.11**	0.04	2	0	0	2	4	**-0.09**	0.03	1	1	1	1	3
constant	**-7.14**	0.69	1	0	0	7	0	**-12.73**	0.81	0	0	1	6	0

Table 4. Selection coefficients (Coef ± SE) in pooled resource selection models for female moose, calculated by season for GPS-collared females from 2008–2010 in the South Canol area of south-central Yukon, Canada. As an indication of variability among individuals, the number of individuals that significantly selected for or against each parameter is shown under ++ or - -, respectively. Individuals with insignificant parameters in the model are shown under + and -; n/a refers to number of animals without a parameter. Significant coefficients are in bold.

Season	Late Winter							Calving							Summer						
Model	$E^1 + A^1 + P^1 + L^1$							E + A + P + L							E + A + P + L						
	Coef	SE	+ +	+	-	- -	n/a	Coef	SE	+ +	+	-	- -	n/a	Coef	SE	+ +	+	-	- -	n/a
Elevation (km)	**24.68**	4.99	6	0	1	0	0	-0.21	7.42	5	3	2	3	0	2.54	3.63	4	1	2	3	0
Elevation^2 (km)	**-10.70**	2.58	0	1	0	6	0	-4.06	4.12	3	1	4	5	0	-1.27	1.69	2	3	1	4	0
Eastness	**0.11**	0.05	3	1	0	3	0	0.00	0.05	4	3	1	5	0	0.02	0.04	2	1	2	5	0
Northness	**-0.17**	0.05	3	0	1	3	0	-0.09	0.05	5	1	3	4	0	-0.06	0.04	3	2	1	4	0
Wolf Risk	0.02	0.06	2	1	1	3	0	0.00	0.14	5	1	2	5	0	0.00	0.09	3	2	2	3	0
Bear Risk								**1.55**	0.37	7	3	1	2	0	0.07	0.12	5	0	2	3	0
Conifer	**-0.10**	0.04	1	1	0	5	0	**-0.61**	0.09	1	1	3	8	0	**-0.11**	0.05	3	2	1	4	0
Alpine	0.00	0.00	0	0	1	0	6	**0.21**	0.10	1	3	0	1	8	**-0.35**	0.06	0	0	0	2	8
Lowland Shrub	0.09	0.05	5	1	0	1	0	0.14	0.09	7	4	1	1	0	0.04	0.04	1	3	4	2	0
Upland Shrub	-0.01	0.02	1	0	1	1	4	**0.54**	0.11	3	3	0	0	7	**0.32**	0.05	3	2	0	0	5
Mixed Wood	-0.05	0.05	1	1	2	3	0	**0.13**	0.06	3	4	4	0	2	**0.15**	0.05	5	1	2	1	1
Riparian	**0.18**	0.06	5	0	0	2	0	-0.01	0.09	5	4	3	1	0	**0.27**	0.07	6	1	1	2	0
Water	0.00	0.00	0	0	0	0	7	**-0.24**	0.07	0	2	2	2	7	**-0.16**	0.05	0	1	1	3	5
Lowland Open	**-0.10**	0.02	0	0	0	1	6	**-0.15**	0.05	0	0	2	2	9	**-0.15**	0.04	0	0	1	2	7
constant	**-15.71**	2.49	0	1	0	6	0	-0.10	3.47	2	2	3	6	0	-3.39	1.89	2	2	1	5	0

[1] E = elevation, A = aspect (eastness and northness), P = predation risk (wolf and grizzly bear), L = land-cover class, H = harvest vulnerability.

Table 4 continued....

Table 4. continued

Season	Rut							Early Winter						
Model	E + A + P + L + H							E + A + P + L						
	Coef	SE	+ +	+	-	- -	n/a	Coef	SE	+ +	+	-	- -	n/a
Elevation (km)	**10.31**	1.76	5	2	0	3	0	**6.97**	0.69	8	0	0	2	0
Elevation^2 (km)	**-4.06**	0.72	3	0	2	5	0	**-3.30**	0.28	1	1	0	8	0
Eastness	**-0.06**	0.02	2	2	0	6	0	**-0.11**	0.02	2	1	2	5	0
Northness	-0.04	0.02	4	0	0	6	0	**0.10**	0.03	7	0	0	3	0
Wolf Risk	**0.50**	0.08	6	2	2	0	0	**0.07**	0.03	4	2	0	4	0
Bear Risk	-0.05	0.08	5	2	2	1	0							
Harvest risk														
Conifer	**-0.24**	0.03	1	1	2	6	0	**-0.64**	0.04	0	0	1	9	0
Alpine	**-0.34**	0.08	2	1	1	4	2	**-0.79**	0.09	1	2	0	6	1
Lowland Shrub	-0.02	0.07	7	0	0	3	0	**0.22**	0.03	7	0	2	1	0
Upland Shrub	**0.42**	0.07	7	1	0	2	0	**0.49**	0.05	6	2	1	1	0
Mixed Wood	-0.11	0.06	2	2	2	4	0	**-0.24**	0.05	1	1	3	5	0
Riparian	**0.38**	0.05	7	1	0	2	0	**0.66**	0.03	9	1	0	0	0
Water	**-0.14**	0.04	1	1	1	2	5	**-0.10**	0.02	0	0	1	2	7
Lowland Open	0.04	0.04	2	1	1	2	4	0.39	0.05	5	0	1	1	3
constant	**-8.49**	1.06	2	1	1	6	0	**-5.30**	0.42	1	0	0	9	0

bear risk during the Calving season; wolf risk was often insignificant or variable between sexes.

Conifer was strongly avoided by both sexes in all seasons. Males also avoided Alpine except in Summer, whereas females selected for Alpine during Calving, but avoided it from Summer through Early Winter. Both sexes selected Upland Shrub areas in almost all seasons. The Lowland Shrub class was selected by both sexes in Early Winter and by males in the 2 seasons afterward (Late Winter and Calving). Mixed Wood was almost always avoided by males, but selected by female moose during Calving and Summer. Both sexes usually selected for Riparian areas (although females did not during Calving). Female moose selected against Water, and the influence of Water varied across seasons for males, with positive selection for frozen waterways in Early and Late Winter.

For models developed for females with and without a calf, there were only 7 valid models after k-fold cross-validation (out of 24; 6 models for each animal) to explain habitat selection during Calving for 4 females with known calf status; 6 of these models had AIC_c weights < 0.95. Three models would have resulted from model averaging, but given the low sample sizes (2 females with calves, 2 without), we did not pursue further analysis. The only consistency observed in those models was selection for Lowland Shrub by all 4 females. Additionally, females with calves selected for higher elevations while avoiding Mixed Wood. Females without a calf selected Mixed Wood and avoided Riparian.

Variation in seasonal habitat selection among individual moose

For the 24 individual moose in our study, 82 final models described seasonal habitat selection. In addition to all topographic and predation coefficients, there were at least 3 land-cover classes (i.e., Conifer, Lowland Shrub, Riparian) in all final models. As mentioned above, in the averaging process for sex-specific pooled models, Late Winter had the fewest explanatory models and the fewest individuals; Calving had the most. In general, there were more individual models during Summer and Rut for males than for females.

There were some strong seasonal trends among individual moose within a sex (Tables 3, 4), and female patterns tended to be more variable than males. Responses to east-facing slopes, wolf risk, and the Water and Lowland Open classes were highly variable among individuals. During Late Winter, most individuals selected for Riparian areas and avoided Conifer stands. Most males avoided north-facing slopes, but responses to aspect were highly disparate among females. At this time, when snow was presumed to be deepest, most females selected for Lowland Shrub areas, whereas males exhibited more variability. During the Calving season, most individuals continued to avoid Conifer and were often in high bear-risk areas. Most males continued to avoid north-facing slopes and selected Lowland and Upland Shrub areas, whereas females demonstrated more variation in habitat use during Calving. In Summer, male moose selected more consistently for mid-elevations than during Late Winter and Calving, and avoided Conifer cover. The selection for Conifer and Lowland Shrub classes was more variable among individual females in Summer than in other seasons. Not surprisingly, individuals of both sexes displayed most similarities during the breeding season and the post-rut period. During Rut and Early Winter, most individuals selected Upland Shrub and Riparian areas while strongly avoiding Conifer. The majority of males avoided Alpine and Mixed Wood during Rut, and most moose (both sexes) selected for Lowland Shrub in Early Winter.

DISCUSSION

Moose are a keystone species of northern boreal forests, playing important roles in predator-prey dynamics and forest succession (Molvar et al. 1993, Danell et al. 1998). The large geographic range of moose is a reflection of their ability to utilize a wide variety of habitats. Elevation, aspect, predation risk, and land cover all had significant effects on seasonal habitat selection by moose in the South Canol area. At the resolution of this study, seasonal changes appeared to affect resource selection by moose in the South Canol area more than differences between sexes or reproductive status (females with and without calves).

Elevational differences in temperature and soil moisture influence habitat selection through associated changes in vegetation, snow depth, and thermal conditions. In an effort to balance energetic demands, moose respond to the changing quantity and quality of forage species and accessibility to forage and cover that are found along elevation gradients (Stumph and Wright 2007). Resource selection for male moose in our study was influenced by elevation in all seasons, and most consistently among individuals in Summer, Rut, and Early Winter. Access to the higher elevations in these seasons (as reflected in use patterns, McCulley et al. 2017b) may play an important role in the survival strategies of male moose in south-central Yukon. Ballard et al. (1991) reported that upland sites had higher quantities of browse, but lower elevation sites had greater availability as winter progressed. In our study area, upland areas may provide similar opportunities for moose to maximize forage intake in the seasons surrounding Rut, and to build adequate fat reserves before the snowpack forces them to descend in Late Winter. Like males, females also selected for mid-elevations in most seasons, except during Calving and Summer when selection patterns varied among individuals. Oehlers et al. (2011) reported moose calving at lower elevations in southeast Alaska, which contrasted with those in interior Alaska that chose high-elevation birth sites (Bowyer et al. 1999). Female moose in southeast British Columbia were categorized as “climbers” or “non-climbers” during the Calving season (Poole et al. 2007). These examples, as well as the variation in individual models in our study, highlight the unpredictable nature of birth-site selection by female moose during Calving.

Similar to elevation, aspect can strongly influence ambient temperature and soil moisture. South-facing slopes receive the most solar radiation and are the first to green up at northern latitudes; north-facing slopes tend to be cooler and moister throughout the year. East and west aspects increase solar insolation at different times of the year. In the South Canol area, we observed that males (group and individually) selected for west aspects during Calving and Early Winter, and females selected northwest aspects in Early Winter, but with more individual variation. This selection may reflect a need to minimize heat stress during times of the year when moose have highly insulative winter pelage and temperatures may occasionally be relatively warm. Males and females selected southeast aspects during Late Winter, when males in particular must minimize energy losses in order to survive until spring. Similar to our findings in Late Winter, moose in southeast British Columbia preferred gentler slopes with high solar insolation during late winter (Poole and Stuart-Smith 2006), and moose in Montana selected south- and west-facing aspects in late winter (Langley 1993). Selection of south-facing slopes may allow moose to key in on spring green-up (e.g., Merkle et al. 2016). Bowyer et al. (1999) reported that female moose preferred to give birth on southeast exposures where soils were drier and forage was of higher quality.

We defined predation risk by combining habitat information from our study area with seasonal RSFs from GPS-collared wolves and grizzly bears in the Besa-Prophet area of northern British Columbia. These models were assumed to be compatible with our landscape based on similar predator species, climate, and mountainous topography. The predation risk surfaces, however, should be verified with local predator data as they become available. The ungulate prey base in the South Canol area is not as diverse as that in the Besa-Prophet area of northern British Columbia, and hence, predators could potentially focus more on moose in the South Canol area. Black bears, for which there are no density estimates in Yukon (R. Maraj, Yukon Department of Environment, pers. comm.), were assumed to have a relatively low (although not quantified) impact on adult animals, and this premise also should be verified. Reducing exposure to mortality risk has obvious benefits to individual moose survival (and their calves). Associated with predators, there also can be energetic costs such as reduced foraging efficiency caused by increased vigilance or movement, and by choosing safer habitats that may have less forage (Molvar and Bowyer 1994, White and Berger 2001, Montgomery et al. 2013). Additionally, Kunkel and Pletcher (2000) noted that wolf kill rates increased with increasing distance to cover, decreasing road density, increasing trail and stream density, and increasing wolf density.

Exposure to predation risk varied seasonally, but not between males and females, yet individual responses were varied. Contrary to our hypothesis, females did not avoid predation risk during the Calving season. Both sexes showed positive selection for areas with higher bear risk during Calving, presumably by taking advantage of areas with earlier green-up that were also frequented by bears (Bastille-Rousseau et al. 2011). During Late Winter, females with calves used areas with significantly less wolf risk than females without calves. Because of their shorter legs, moose calves are more vulnerable in deep snow than adults (Peterson and Allen 1974, Peterson 1977). Females with calves are known to reduce wolf risk by staying closer to cover, which helps make calves less visible and where snow depths may be lower (White and Berger 2001). Male moose in the South Canol area avoided wolf risk during Rut, but their exposure to wolf risk (as indexed by average relative risk; Fig. 2) was slightly higher during Rut than during the Calving season or Summer. During the moose breeding season, wolf pups (and the associated adults) are more mobile than earlier in the growing season, potentially increasing risk to moose (Mech 1970, Mills et al. 2008). During Rut, exposure to bear risk for both sexes was significantly higher than during Summer. This is likely because bears move up in elevation during late summer and fall to target the rich berry crop usually available in subalpine areas. By Early Winter, exposure to bear risk was negligible as bears hibernated. Average exposure to wolf risk (Fig. 2) dropped significantly; the positive selection coefficients in the pooled models for both sexes may indicate simply those areas also frequented by wolves rather than high-risk areas, per se.

In Yukon, most harvest targets male moose and most hunting pressure occurs in September (Yukon Department of Environment 2008).We expected males to select areas with lower harvest vulnerability during Rut and analysis confirmed that males as a group minimized harvest vulnerability. The individual responses, however, were variable and only 50% of males avoided this risk. The selection for less-accessible higher elevations during Rut may have served to reduce exposure to harvest vulnerability as well as predation risk. Because of limited road access, most moose harvested in our study area were harvested at lower elevations, often on or within 500 m of large waterways. Similarly in Quebec, density of hunting camps, length of large rivers, and surface area of lakes had the greatest effects on harvest vulnerability (Courtois and Beaumont 1999). Male moose also may make fine-scale adjustments to avoid detection, but such selection or avoidance would be difficult to determine at the resolution (25 m) of our study (Courtois and Beaumont 1999, Laurian et al. 2000). Vulnerability and response to harvest risk can vary depending on age and experience of the moose. In our study, only mature males were collared and individuals likely had several years' experience avoiding detection by predators or humans. Habitat selection by younger males may differ from our observations.

We expected moose to maximize forage intake during the growing season (Belovsky 1978) and minimize energy losses in winter, recognizing that male and female moose would likely use different strategies to meet those ends. We assumed a forage-based strategy would be indicated by strong selection for shrub-dominated land-cover classes, whereas selection of Conifer would indicate a greater need for cover. All males avoided Conifer throughout the year, as did females as a group, although individuals had variable responses. The interpretation of strategies used for forage and cover may be confounded by the scale of selection and because Conifer represented a large proportion of the study area (McCulley et al. 2017b). Although Conifer was avoided, it was used often because of its abundance on the landscape. Poole and Stuart-Smith (2006) reported that moose selected higher crown closure at the landscape scale, whereas others have observed selection for conifer stands at finer scales related to thermal cover (McNicol and Gilbert 1978), forage diversity (Peek 1997), and predation risk (Bowyer et al. 1999, Dussault et al. 2004, Bjorneraas et al. 2012). Both sexes selected for shrub-dominated land-cover (i.e., Upland Shrub, Riparian, or Lowland Shrub) throughout most of the year, with highest selection for Upland Shrub during the Calving season through Rut, and for Riparian areas in Early and Late Winter; most individuals also selected for Lowland Shrub from Early Winter through Calving. The elevational gradient encompassed by these communities likely enabled all moose to seasonally target areas with highest food quality and forage biomass.

We expected selection patterns of both sexes to be most similar during the breeding season and most different during parturition and lactation (Miquelle et al. 1992, Oehlers et al. 2011). Indeed, during Rut males and females selected strongly for Upland Shrub and Riparian, while avoiding Conifer, Alpine, and Water. Conversely, during Calving they generally differed in response to Alpine, Riparian, Water, and Lowland Open classes. Interestingly, females did not select for Riparian areas during the Calving season which was surprising given that proximity to water is an important characteristic of birth sites in other areas (Oehlers et al. 2011). We defined riparian zones as areas within 100 m (4 pixels) of large rivers and lakes and only 25 m (1 pixel) from small streams, so perhaps females were able to locate birth sites outside of the riparian zone as we defined it, but still with adequate access to water.

Land-cover classification based on satellite imagery is efficient and was particularly valuable in our study which spanned a remote and isolated area covering 14% of Yukon's landmass. An existing EOSD land-cover classification for Yukon had a species-appropriate resolution (25 m) and was based on digital imagery collected within 8 years of the study. By merging some of the 24 classes into 8, we reduced the chances for misclassification. The variation encompassed by each land-cover class, however, may have contributed to the variation observed among individuals and could be important in fine-scale selection by moose.

Variation in selection patterns may have been confounded by the GPS locations for each individual. Although we could not adjust for potential bias in fix rates, we reduced bias toward particular individuals with more location fixes by developing selection models per individual, and requiring a minimum of 100 locations per individual per season. We also had the opportunity to monitor a stationary fully-functioning GPS collar for 11 months (after an animal died) to assess GPS field accuracy; mean distance between fixes was 7.9 ± 0.25 m. Given the resolution of the land-cover data, the land-cover class associated with each location point was fairly precise.

Some low fix-acquisition rates may have introduced location bias, particularly if missed fixes were more likely to occur in some land-cover classes. Although we were unable to correct for land-cover or terrain characteristics, habitat transition probabilities, or fixes lost across geographical space (Frair et al. 2004, 2010; Nielson et al. 2009), it is most likely that any biases are associated with under-representing the use of closed conifer forests and perhaps north-facing aspects. There was, however, no significant relationship between fix -rate success and the proportion of Conifer land cover within annual ranges across collared individuals or among individuals with collars from the same manufacturer. Lowest (18% of annual range) and highest (66%) Conifer cover were both observed with fix rates > 88%. Nonetheless, our habitat selection coefficients should be interpreted with some caution in the possible case of alternative biases.

In summary, moose in south-central Yukon altered their selection patterns in response to seasonal changes typical of northern boreal forests. Differential seasonal selection was observed within individuals and groups. Differences between the sexes in exposure to risk were not supported by our data, but may occur at finer spatial and temporal scales than in our study. The differences in the selection coefficients of individual and pooled models underscored the variety of moose-habitat relations in the South Canol area. Pooled models for large non-herding species such as moose may encompass highly variable behaviour among individuals. The "average" moose may not exist (Gillingham and Parker 2008b), yet individual models effectively demonstrate the variability *within* the population of interest (McCulley 2015: Appendix F, G). Relative consistency of individual responses by both sexes supports trends identified by pooled selection coefficients, and detects trends between sexes.

Most individual variation occurred during the growing season (Calving and Summer) and the least amount during Late Winter, suggesting that climatic factors limited the options available to moose during the most resource-constrained season. This observation may have important implications to moose populations in Yukon, where climate change is occurring at a faster rate than in more southerly moose ranges (ACIA 2005). Moose experience increased heat stress, higher parasitic loads, more malnutrition, and greater wolf predation in warmer climates (Rempel 2011), with declines reported in certain populations at the southern extent of moose range (e.g., Post et al.1999, Murray et al. 2006). Because moose respond to climatic factors at large scales (Hallett et al. 2004), continual habitat use and population assessments are encouraged to evaluate the broad expanse of northern moose populations for which less is known about potential climatic impacts.

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