

YUKON MOOSE: II. RANGE SIZES, MOVEMENT RATES, AND USE OF ELEVATION AND LAND COVER BY MALES AND FEMALES

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ABSTRACT: Moose (*Alces alces*), as a focal species in many northern communities, are increasingly subjected to anthropogenic activities. We studied range use by moose (males and females with and without calves) to enable more effective land-use planning in south-central Yukon. We detected seasonal differences in range sizes, movement rates, and use of elevation and land cover by global positioning system (GPS)-collared individuals, reflecting the responses of individuals to changing resource availability that is characteristic of boreal landscapes. During winter, moose in the South Canol area generally used smaller ranges at lower elevations and moved at lower rates within them, presumably limited by snow depths. They moved up in elevation throughout summer, reaching maximum elevations during rut and early winter. Moose used conifer stands, which were prevalent on the landscape, more than any other land-cover class throughout the year. Their use of upland and lowland shrub classes varied with season, with highest combined use of shrub-dominated land cover in early and late winter, likely reflecting the importance of shrubs as winter forage. We were unable to identify significant differences between the sexes or relative to reproductive status (i.e., calf presence). Differences between these groups in meeting requirements for forage and cover may be more discrete at the finer scale of microsite characteristics.

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Home range, as the area an animal routinely uses to meet its needs (Burt 1943), is a useful concept for studying animal use of the landscape, presuming that animals choose to live where their fitness is maximized within the constraints imposed by their environment (Mitchell and Powell 2012). In so doing, they regularly exploit and update information, such that the home range represents the interplay between the environment and the animal's understanding of that environment (Powell and Mitchell 2012). Animals choose home ranges and places within the home range to access critical resources of food, cover, and opportunities to

reproduce, while minimizing risks of mortality. Changing environmental conditions affect distribution, quantity, quality, and accessibility of forage and cover over the landscape (Telfer 1970, Van Ballenberghe and Peek 1971, Coady 1974). Resources are rarely distributed evenly over time or space, so animals move to access these resources as availability changes. Thus, movement rates affect both range size and intensity of use (Dussault et al. 2005a).

The widespread geographic range of moose (*Alces alces*) reflects the ability of this species to use a variety of successional stages found throughout the world's boreal

forests. With their large body size, moose are relatively well-adapted to the deep snow, cold temperatures, and predators found in northern boreal habitats. They frequent numerous stand-cover types and age classes that provide early seral areas for food and mature coniferous cover (Telfer 1984). Conifer species are used primarily as cover to moderate extremes of heat, cold, wind, and deep snow, and as security from predators (Timmermann and McNicol 1988, Balsom et al. 1996, Mysterud and Ostbye 1999). Use of shrub-dominated areas by moose often corresponds with foraging activity because shrub species make up the majority (>60%) of their annual diet (Renecker and Schwartz 2007). Mixed-wood areas, interspersed with both conifers and deciduous trees and shrubs, provide a mix of forage and cover, potentially important to both sexes when mobility may be limited. Riparian areas also provide a variety of tree and shrub species used for cover and forage. Although alpine areas are generally not considered suitable for moose, riparian zones and wetter areas at high elevations may contain highly-selected *Salix* species, which are preferred compared to other shrubs such as *Betula* spp. (Van Balenbergh et al. 1989, Dungan and Wright 2005) that grow on drier sites. The proximity to a water source can affect movements and range use by moose, as when females select birthing sites in spring (Poole et al. 2007). During summer, aquatic plants associated with wetlands and littoral zones may be important sources of sodium and other limiting nutrients, and influence local foraging strategies (Belovsky 1981, Belovsky and Jordan 1981, Fraser et al. 1982). In winter, frozen waterways function as movement corridors for moose and wolves (*Canis lupus*) that pursue them (Kunkel and Pletcher 2000).

As with other ungulates, foraging behaviour of moose is influenced by differences in forage quality, quantity, and accessibility

(Andersen and Saether 1992). Moose feed on a wide variety of plant species to meet nutritional requirements (Miquelle and Jordan 1979), and require large amounts of forage (e.g., ~20 kg per day for a 450-kg animal in summer) because of their large body size (Renecker and Hudson 1992, Renecker and Schwartz 2007, Schwartz and Renecker 2007). Moose with access to high quantities of forage travel less than those in areas where forage is more dispersed (Timmermann and McNicol 1988). Forage quality influences daily activity, range use, and foraging patterns (Saether and Andersen 1990). Not surprisingly then, there can be wide variation in home-range sizes among individuals and between seasons (Phillips et al. 1973, Addison et al. 1980). In addition, periodic disturbances, such as wildfires, change the availability and abundance of forage and cover (Cederlund and Sand 1994).

Body size, age, and sex can influence home-range size because of differing nutritional requirements (e.g., increased energy and protein demands during growth, lactation, and accretion of body reserves prior to winter) and social activities between sexes and age groups. Movements between seasonal ranges are usually related to reproductive events (e.g., rut, parturition) and environmental changes (e.g., snow depth). Human activities can also influence the quality of environments available to moose and directly increase mortality risk. Increased human access to previously undisturbed areas can increase mortality from vehicle collisions (McLellan and Shackleton 1988, Forman and Alexander 1998, Trombulak and Frissell 2000), as well as hunting pressure (Courtois and Beaumont 1999, James and Stuart-Smith 2000, Crichton et al. 2004). Anthropogenic influences are likely to become more prominent as human density increases and the spatial extent of resource extraction and recreational activities expands.

For sexually dimorphic ungulates such as moose, potential explanations for sexual segregation and differential use of the landscape correspond to 3 general categories of survival strategies: reproductive hypotheses, sexual dimorphism itself, and social factors (Main et al. 1996). Reproductive hypotheses stem from the different roles of the sexes and associated nutritional requirements. From a predation-risk standpoint, males should maximize body condition before rut, even if predation risk increases, whereas females should maximize security of calves provided that minimum resource requirements are met (Main and Coblenz 1990). Sexual dimorphism, characterized by allometric and physiological differences, also results in differing nutritional requirements and vulnerability to predation related to gastrocentric, activity-budget, and weather-sensitivity hypotheses. Males should use areas that maximize forage intake because of larger rumen size and the ability to digest lower-quality forage, in contrast to females (with smaller rumen size) that should target areas with higher-quality forage, particularly during late gestation and lactation (Barboza and Bowyer 2000). Females, because of their smaller gut capacity, should spend more time foraging than males that spend more time at rest and ruminating (Ruckstuhl 1998). In winter, males are likely to be more sensitive to weather because of their higher absolute heat losses relative to intake rates (Conradt et al. 2000). Finally, social factors may account for variable aggregation and segregation among cohorts throughout the year. The difficulty in explaining differential use of the landscape between the sexes is often confounded because these survival strategies may not be mutually exclusive.

Moose are found throughout Yukon, where 2 subspecies (*A. a. agigas*, *A. a. andersoni*) are believed to overlap (Bubenik 2007). Despite considerable study of range use by

moose in other areas of Canada and Alaska (Dussault et al. 2001, Dussault et al. 2005a, b, Maier et al. 2005, Gillingham and Parker 2008, Mabelle et al. 2012), few studies have investigated habitat requirements and limiting factors of moose in Yukon (e.g., Mauer 1998, Hayes and Harestad 2000, Hayes et al. 2000). The low productivity and population density of moose, and a much smaller human population are somewhat unique to the Yukon and make comparisons with certain Alaskan and Canadian studies difficult. Little is known about habitat use and distribution of Yukon moose outside the early winter, post-rut period (Nov–early Dec) when most human harvest occurs, and no rigorous studies to differentiate between males and females have been done. South-central Yukon currently has limited access and few industrial activities, but considerable potential for resource extraction with a large population centre relatively close by that may result in more disturbance and access into prime moose habitat. This area provided the opportunity to study group-specific (i.e., males, females with calves, and females without calves) range use and movements to guide resource management in light of increased access and resource development in remote moose habitats.

We initially defined habitat selection patterns of moose (McCulley et al. 2017a) in the South Canol area of south-central Yukon to help clarify the process by which animals choose habitat attributes in relation to their availability and in combination with other attributes. In particular, resource-selection patterns help to interpret the relative importance of different resources, and in combination with behavioral information, explain habitat use. Habitat use by individual moose likely varies in response to numerous factors including differential habitat availability within a heterogeneous landscape, different preferences or requirements of males and females, and predator distribution.

Our goal was to measure and describe habitat use of moose to assess habitat value using range designations and biophysical characteristics. We used global positioning systems (GPS) and geographic information systems (GIS) to examine the effect of seasonal variation and sex (including the effect of calf presence on females) on home-range size, movement rates, and elevation use by adult moose. In addition, we analyzed land-cover composition of ranges at seasonal, annual, and landscape scales to see how use changed over time and space. We predicted that seasonal ranges would be largest in summer when movement was least restricted by snow depth. We expected that seasonal ranges and movement rates of female moose with calves would be smallest during the calving season when newborn calves have limited mobility and are at greatest risk of predation. Females without calves and male moose were expected to have the smallest ranges and movement rates during late winter when snow is presumably deepest and body condition

poorest. Additionally, because of their larger size and higher absolute energetic needs, the annual ranges and movement rates of males were expected to be greater than those of females. We also expected female moose to use more cover in all seasons to reduce exposure of calves to predation risk. The ranges of male and female moose were not expected to overlap outside of the breeding 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 almost 35,000 km², 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). It fell primarily within the traditional territory of the Teslin Tlingit First Nation and also included portions of the Ta’an Kwäch’an, Kwanlin Dun, and Kaska traditional territories. The South Canol area

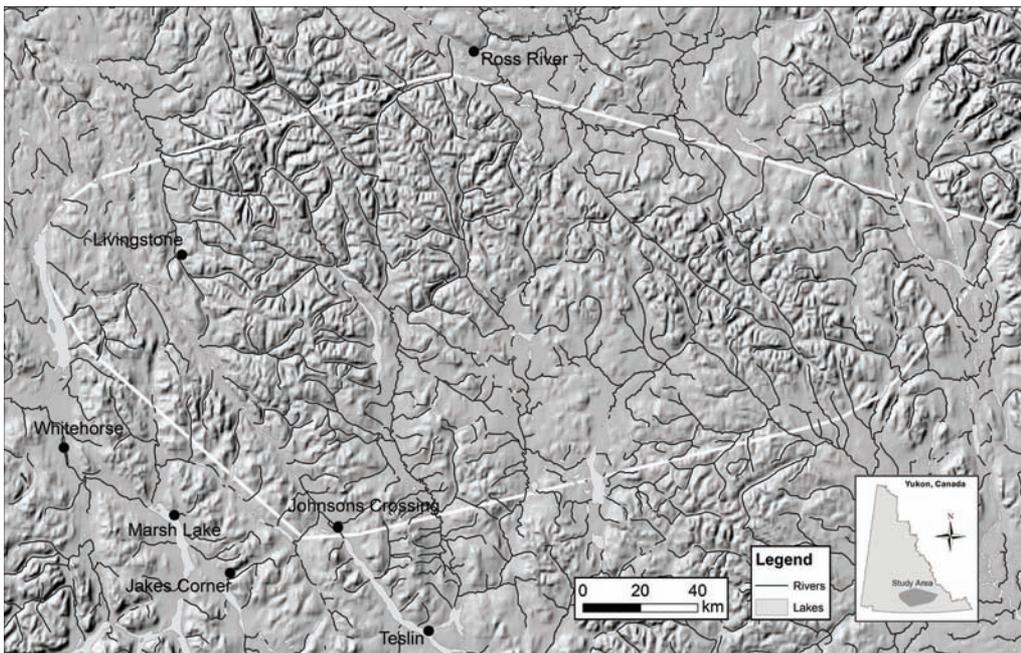


Fig. 1. South Canol moose study area located in south-central Yukon, Canada.

was in the Boreal Cordillera Ecozone and included 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 bisected by small rivers. The Southern Lakes Ecoregion is characterized by bisected plateaus, rolling hills, and broad valleys occupied by lakes and rivers (Yukon Ecoregions Working Group 2004). The entire area was within the sporadic discontinuous permafrost zone. Shrub and dwarf shrub tundra vegetation occurred above 1,350 m above sea level (a.s.l.); coniferous and mixed forests occurred below 1,350 m a.s.l.

A 2007 survey reported the average population density within a 6,735-km² core portion of the study area was 241 moose/1,000 km², which was higher than the Yukon average of 158 moose/1,000 km². There were approximately 22 calves, 18 yearlings, and 76 males for every 100 adult females (Florkiewicz et al. 2008). Grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and wolves were the principal predators in this ecosystem, with densities estimated as 8–12 wolves/1,000 km² (R. Ward, Yukon Department of Environment, pers. comm.) and 15.2 grizzly bears/1000 km² (R. Florkiewicz, Yukon Department of Environment, pers. comm.) during our study. Black bear densities were unknown but assumed to have less impact on adult male and female moose, as they tend to prey on calves (Ballard 1992). The South Canol Road extends from Johnson's Crossing to Ross River and provided access through the eastern portion of the study area. The Pelly Mountains Ecoregion is considered rich in mineral deposits (Yukon Ecoregions Working Group 2004); however, only one hard-rock mineral claim was active (Tintina Mines Ltd.) during the study. An exploration road was upgraded

and extended 76 km from the South Canol Road to Red (Slate) Mountain within the study area. The 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 located 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–27 March 2008 and fitted with GPS collars (15 collars: Lotek GPS4400MARG, New Market, Ontario, Canada; 12 collars: Habit Research Inc. (HRI), Victoria, British Columbia, Canada). Captures were conducted by Yukon Department of Environment personnel with assistance from the Teslin Tlingit Council. The GPS collars were programmed to acquire locations 6–8 times per day (Lotek every 4 or 5 h; HRI every 3 h) and periodically uploaded data to the ARGOS satellite (Lotek every 2 weeks; HRI every 24 h); 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 infrequent errant location points that were likely the result of GPS errors. These were mostly consecutive fixes in which the animal moved an impossibly long distance, given the time between 4- or 5-h fixes, and immediately returned to the initial location. Aerial flights to assess calf survival (and calf status of females) occurred 3 times during each of 2 “biological years” (mid-Jun, Oct–Nov, Mar) beginning in 2008 and ending in March 2010.

Annual and seasonal ranges, movement rates and elevation use

We defined 5 seasons for moose based on life history and biological criteria: 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 corresponded with the timing of seasons in other moose studies in Yukon, Alaska, and British Columbia (Larsen et al. 1989, Miquelle et al. 1992, Gillingham and Parker 2008). As in British Columbia, parturient females become solitary and the onset of plant greening occurs during the Calving season; Summer extends from plant green-up through peak vegetation biomass to the start of plant senescence; senescence of vegetation occurs during the Rut season when moose form mixed sex groups and females come into estrus; sex-specific groups form in Winter following rut; and movement rates decline to lowest levels in Late Winter (Gillingham and Parker 2008). 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. We set 100 locations as a minimum for individual moose to be included in calculations of range size, movement rate, and elevation use in each season. Although arbitrary, given fix schedules and success, conservatively this represented a minimum of approximately 50% of possible fixes for the shortest seasons.

We estimated annual and seasonal range size (km²) for each animal from GPS locations using both the 100% minimum convex polygon (MCP) method and a 95% fixed kernel density estimate (with quartic approximation of a true Gaussian kernel function) with Hawth's Analysis Tools in ArcMap (ESRI 2006). We recognize that MCPs, which link use points on the outside edges of a convex polygon encompassing all points, tend to overestimate range sizes for animals that have infrequent movements away from a centralized area. Kernels, as (a) smaller nested area(s) within the MCP, work well for species that have more than one area of concentrated

use, but may exclude areas where movements take place between concentrated use areas and include substantial 'buffer' areas around high density locations. Even with the limitations of these techniques, both are adequate for testing comparisons of areal use and to explore changes in space-use patterns over time and space (e.g., Signer et al. 2015). We report both MCP and 95% kernel ranges because they are the simplest and most widely applied approaches (Signer et al. 2015), which facilitate comparisons with studies in other regions. Only complete years (2008: 15 May 2008–14 May 2009; 2009: 15 May 2009–14 May 2010) were used to calculate annual home-range sizes. If an individual had 2 complete years available, we calculated the average size of both years. Average seasonal MCP and kernel home-range sizes were determined for each of the 4 groups (males, all females, females with calves, and females without calves).

To delineate a landscape MCP, we first identified available points for each use location by selecting 5 random points from within a buffer surrounding each location point. The radius of the buffer was determined from the 95th percentile movement distance of each individual in each season (Arthur et al. 1996). This buffer represents the maximum distance that an animal would likely travel, excluding rare excursions, between consecutive GPS locations, and was used to not underrepresent availability if an animal chose not to move very far between GPS fixes. We then calculated a movement buffer around the used and available points of all moose based on the average movement rate of each group. The buffer edge was used to define the landscape MCP, which represented the area that was available to all moose in this study (i.e., first-order selection based on landscape features; Johnson 1980).

We examined movement by calculating distance moved between consecutive

fixes and dividing this by the fix interval to produce a movement rate (m/h). For each location, we extracted elevation from a digital elevation model (DEM from Environment Yukon, available at http://www.env.gov.yk.ca/publications-maps/geomatics/data/30m_dem.php; ArcMap 9.3, ESRI 2006). We calculated average seasonal and monthly movement rates and elevations used for each individual moose and each group. Monthly values were used to more precisely define when animals changed movements or elevations. For females with the same calf status in both years, all GPS locations were used to determine the average for each season/month (i.e., not the average of averages); otherwise, separate estimates were determined for each year where appropriate.

We used repeated measures 2-way analysis of variance (ANOVA) to investigate the influence of sex and season (or month) on annual and seasonal range size, movement rates, and elevation use. We assessed significant seasonal effects with post-hoc Bonferroni-corrected confidence intervals on marginal means (Margins in Stata version 12, StataCorp 2011). To explore the effect of calf presence on range size, movement rates, and elevation use of female moose, we calculated 1-way ANOVAs for each season (calf versus no calf). We also calculated 1-way ANOVAs to assess the effect of sex on average annual MCP and kernel range sizes. Because of issues with skew and kurtosis, MCP and kernel data were transformed with inverse and inverse square root transformations, respectively, to meet assumptions of normality (Shapiro-Wilk's test in Stata version 12, StataCorp 2011).

Land-cover composition

We developed a land-cover classification using Earth Observation for Sustainable Development of Forests (EOSD) land-cover information, a DEM, and National

Topographic Data Base (NTDB) hydrology information. EOSD (circa 2002) is interpreted from Landsat-7 imagery with 25-m resolution and is used to classify land-surface elements (e.g., vegetation, water, rock) (Wulder et al. 2003). There were no significant disturbances or anthropogenic landscape modifications between time of Landsat data collection and time of moose locations (R. Florkiewicz, Yukon Department of Environment, pers. comm.). Using remote-sensing software (Geomatica 10.3, PCI Geomatics 2009), we grouped 26 EOSD cover classes (descriptions given in McCulley 2015) with the above-mentioned data sources to produce 8 land-cover classes relevant to moose ecology (Table 1): Conifer, Mixed Wood, Lowland Shrub, Upland Shrub, Alpine, Lowland Open, Water, and Riparian. The EOSD classes were combined based on similarities in vegetation and elevation. Grouping classes also had the added effect of improved accuracy of EOSD data, which approached 75–80% (Marcus Waterreus, Yukon Department of Environment, pers. comm.). Photographic characterization (and some ground verification) of these classes was provided in McCulley (2015). We assumed that classes with a predominance of shrub species and deciduous trees (Lowland and Upland Shrub) had high forage values, and that the Conifer class provided the most cover for shelter. We clipped the raster land-cover classification to each animal's annual and seasonal MCP range, as well as the landscape MCP (Hawth's Analysis Tools, ESRI 2006). We calculated the percent (%) cover of the 8 land-cover classes within each of these ranges (McCulley 2015), and used contingency tables created for each individual to investigate differences between landscape and annual ranges (Dunnnett and Gent 1977). We used repeated measures 2-way ANOVA to investigate whether the use of land-cover classes differed between sexes

Table 1. Description of 8 land-cover classes across the South Canol study area of south-central Yukon, Canada.

Land-cover Class	% of Study Area	Description
Conifer	45	Spruce, pine or subalpine fir covering 75% or more of total basal area.
Mixed Wood	6	A mix of conifers or deciduous trees with neither exceeding 75% of total basal area.
Lowland Shrub	11	Areas below 1,300 m a.s.l. with $\geq 20\%$ vegetative cover of which at least 33% is shrub species. Also includes deciduous trees exceeding 75% of total basal area.
Upland Shrub	12	Areas above 1,300 m a.s.l. with $\geq 20\%$ vegetative cover of which at least 33% is shrub species. Also includes deciduous trees exceeding 75% of total basal area.
Alpine	14	Areas above 1,300 m a.s.l with $\geq 20\%$ vegetative cover. Includes snow, ice, exposed land, and areas with no data above 1,300 m a.s.l. Excludes Upland Shrub.
Lowland Open	3	Areas below 1,300 m a.s.l with $\geq 20\%$ vegetative cover, or exposed land with $< 5\%$ vegetation. Excludes Lowland Shrub.
Water	2	Lakes, ponds, reservoirs, rivers, streams, or creeks.
Riparian	7	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.

¹1-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.

and among seasons. Post-hoc analyses for significant 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 use of land-cover classes differed between females with and without calves during the Calving season. It was necessary to transform data in most land-cover classes (i.e., square root: Alpine, Upland Shrub, Mixed Wood, Water; log: Low Shrub; Box-Cox: Riparian, Low Open). All statistical analyses were performed using Stata (version 12, StataCorp 2011), with significance set at $\alpha = 0.05$.

RESULTS

We retrieved 78,687 valid location points from 24 moose (8 males, 16 females) between 1 March 2008 and 14 May 2010. Fifteen collars provided 2 complete years of location data and 9 others transmitted data for at least 1 full season. Three collars

transmitted for less than 1 season and these animals were removed from the analyses. The mean fix rate success was $88 \pm 4\%$ ($\bar{x} \pm SE$) for males and $66 \pm 7\%$ for females.

South Canol landscape and annual ranges of moose

The study area was 34,953 km² as defined by the landscape MCP analysis. Typical of boreal forest systems, nearly half of the study area was dominated by conifers (*Picea glauca*, *P. mariana*, *Abies lasiocarpa*) (Table 1). Shrubs covered slightly less than 25% of the landscape and were distributed equally between high and low elevations. Alpine areas comprised 14% of the area. Riparian areas, defined by their proximity to water (i.e., within 100 m of large rivers and lakes, or within 25 m of smaller streams) were widely dispersed and covered $< 10\%$ of the landscape. Mixed Wood areas and Water encompassed 6% and 2% of the study area, respectively.

The mean annual 100% MCP home range of male moose was almost 2.5 x larger ($\bar{x} \pm SE = 1,243 \pm 617 \text{ km}^2$, range = 199–4,968 km^2 , coefficient of variation (CV) = 140%, $n = 8$) than that of female moose ($\bar{x} = 502 \pm 150 \text{ km}^2$, range = 142–2,025 km^2 , CV = 104%, $n = 12$); apparent outliers existed for both sexes (Table 2). The 2 largest male ranges were 4,968 km^2 and 2,850 km^2 , 5–9 x that of the next largest estimate; the largest female range was 2,025 km^2 , ~2.7 x the next largest estimate. The mean annual 95% kernel ranges of males and females were more similar in size (males: $\bar{x} = 115 \pm 23 \text{ km}^2$, range = 56–246 km^2 , CV = 58%, $n = 8$; females: $\bar{x} = 81 \pm 10 \text{ km}^2$, range = 37–164 km^2 , CV = 42%, $n = 12$) (Table 2). Animals with the largest annual MCP ranges also had the largest annual kernel ranges. Male and female range sizes were not statistically different (MCP: $F_{1,18} = 1.05$, $P = 0.32$; kernel: $F_{1,18} = 1.95$, $P = 0.18$). Proportions of land-cover classes within individual annual ranges differed from availability

on the landscape (all $\chi^2 > 424$, all $P < 0.001$); thus, home ranges were not located randomly on the landscape (Table 3).

Seasonal ranges and movements

When comparing males and females, we found no significant differences in seasonal range size (MCP: $F_{1,80} = 0.12$, $P = 0.73$; kernel: $F_{1,80} = 2.37$, $P = 0.13$), movement rate (seasonal: $F_{1,80} = 0.05$, $P = 0.83$; monthly: $F_{1,209} = 0.07$, $P = 0.79$), or elevations used (seasonal: $F_{1,76} = 2.17$, $P = 0.15$; monthly: $F_{1,165} = 1.64$, $P = 0.20$) (Table 2). High individual variability existed, particularly in male seasonal ranges that were ~33% more variable than female ranges (CV for MCP ranges = 142% for males and 105% for females; CV for kernel ranges = 46% for males and 35% for females).

Depending on season (and month), differences were found in kernel range sizes ($F_{4,80} = 14.64$, $P < 0.01$), movement rates (season: $F_{4,80} = 42.35$, $P < 0.01$; month: $F_{11,209}$

Table 2. Mean ($\bar{x} \pm SE$) seasonal and annual 100% minimum convex polygon (MCP) and 95% kernel range sizes (km^2) of radio-collared male and female moose, as well as by reproductive status (females with and without calves), in the South Canol study area of south-central Yukon, Canada. Mean values were rounded to the nearest km^2 .

Season	Range Estimator	Males $n = 8$	Females (All ¹)	Females (No calf ²)	Females (Calf ³)
Late Winter	MCP	84 ± 47	85 ± 32	85 ± 32	74 ± 48
	Kernel	18 ± 3	16 ± 2	16 ± 2	10 ± 5
Calving	MCP	195 ± 53	115 ± 40	140 ± 84	117 ± 29
	Kernel	40 ± 5	21 ± 3	23 ± 6	21 ± 3
Summer	MCP	290 ± 196	72 ± 15	48 ± 17	51 ± 11
	Kernel	38 ± 8	25 ± 3	24 ± 6	30 ± 5
Rut	MCP	385 ± 222	133 ± 31	160 ± 75	170 ± 43
	Kernel	62 ± 9	34 ± 3	37 ± 7	38 ± 4
Early Winter	MCP	147 ± 64	172 ± 34	161 ± 37	197 ± 29
	Kernel	36 ± 6	37 ± 3	36 ± 3	44 ± 7
ANNUAL	MCP	1243 ± 617	502 ± 150		
	Kernel	115 ± 23	81 ± 10		

¹Late Winter and Early Winter: $n = 17$; Calving: $n = 22$; Summer and Rut: $n = 14$.

²Late Winter: $n = 14$; Calving and Early Winter: $n = 12$; Summer and Rut: $n = 9$.

³Late Winter: $n = 3$; Calving: $n = 10$; Summer, Rut and Early Winter: $n = 5$.

Table 3. Effects of sex and season on use of 8 land-cover classes by radio-collared moose (n) in the South Canol study area of south-central Yukon, Canada as determined by 2-way repeated measures ANOVA. Significant values are indicated in bold.

Land-cover Class		n	F	df	P
Conifer	Sex:	23	0.12	1, 107	0.733
	Season:	23	9.18	5, 107	<0.001
Lowland Shrub ²	Sex:	23	0.61	1, 107	0.048
	Season:	23	5.25	5, 107	<0.001
Upland Shrub ¹	Sex:	12	0.18	1, 54	0.669
	Season:	12	7.65	5, 54	<0.001
Alpine ²	Sex:	11	4.10	1, 49	0.048
	Season:	11	11.51	5, 49	<0.001
Riparian ³	Sex:	23	0.01	1, 107	0.922
	Season:	23	1.82	5, 107	0.114
Mixed Wood ²	Sex:	23	0.33	1, 107	0.569
	Season:	23	2.39	5, 107	0.043
Lowland Open ³	Sex:	20	0.47	1, 94	0.496
	Season:	20	0.61	5, 94	0.689
Water ²	Sex:	13	0.10	1, 60	0.756
	Season:	13	4.19	5, 60	0.003

¹Log transformation.

²Square root transformation.

³Box-Cox transformation.

= 23.75, $P < 0.01$), and elevations used (season: $F_{4,76} = 17.88$, $P < 0.01$; month: $F_{11,165} = 12.90$, $P < 0.01$); MCP range sizes did not differ ($F_{4,80} = 1.22$, $P = 0.31$). Kernel ranges were smallest in Late Winter (Table 2). Movement rates differed among seasons except between Summer and Rut (as per non-overlapping Bonferroni-corrected post-hoc confidence intervals for all moose). Males had highest rates (136 ± 9 m/h [$\bar{x} \pm SE$]) during Rut and females ($\bar{x} = 115 \pm 8$ m/h) during Summer (Fig. 2A); both sexes had lowest movement rates in Late Winter (Fig. 2A, B). The elevations used by moose declined from November until late winter (Fig. 2D). Calf presence was not related to seasonal range size (MCP: all $P \geq 0.20$, kernel: all $P \geq 0.28$), movement rates (all $P \geq 0.28$, Fig. 3A, B), or elevation use (all $P \geq 0.21$, Fig. 3C, D) of females across seasons, although the small

sample ($n = 5$) of females with calves tended to move at lower rates during the winter months (Fig. 3B).

The proportional use of land-cover classes was not affected by sex, with the slight exceptions in Alpine and Lowland Shrub classes (Table 3). Annual ranges of males had a higher proportion of Alpine than those of females. Season had a significant influence on use of all land-cover classes except in Riparian and Low Open areas. In annual and all seasonal ranges, except in Early Winter, moose used Conifer stands more than any other land-cover class (Fig. 4). The importance of Upland Shrub (e.g., Early Winter) and Lowland Shrub (e.g., Late Winter) varied with season. There were no differences in use of land-cover classes by females with and without calves during Calving (all $P \geq 0.22$, Fig. 5).

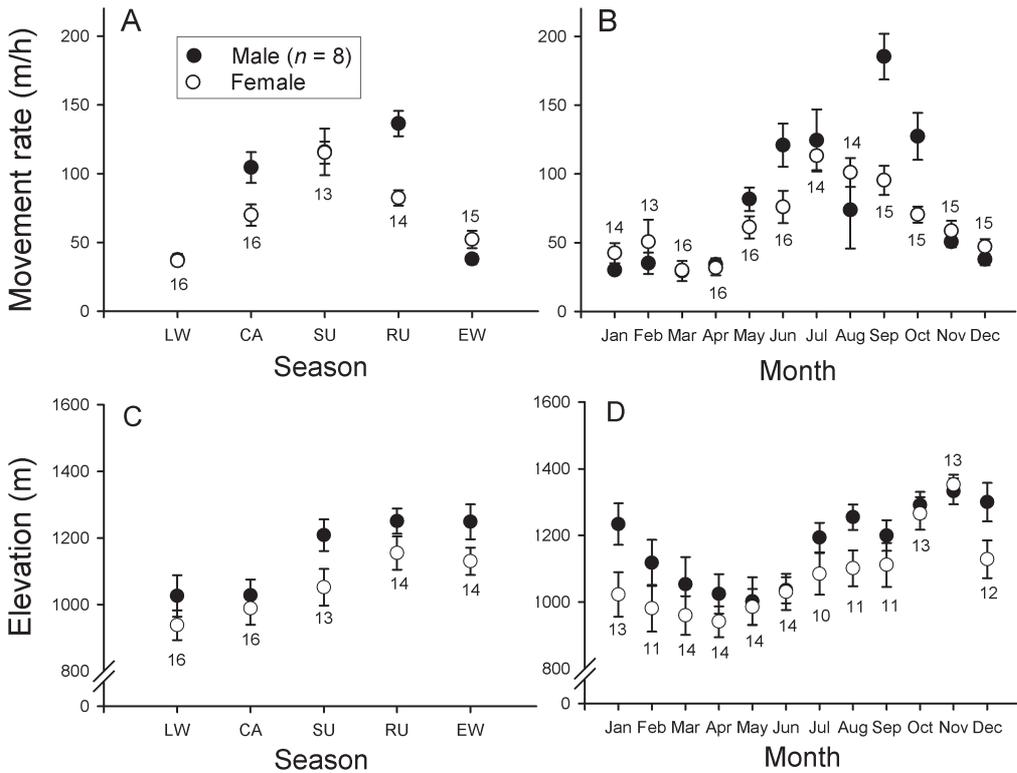


Fig. 2. Average ($\bar{x} \pm SE$) movement rates (m/h) and use of elevation by season (A, C) and month (B, D) for male and female radio-collared moose in the South Canol study area of south-central Yukon, Canada. Numbers shown are sample sizes of female moose. LW = Late Winter, CA = Calving, SU = Summer, RU = Rut, EW = Early Winter.

DISCUSSION

Moose exhibit high variability in habitat use (Osko et al. 2004, Mansson et al. 2007, Poole et al. 2007, Leblond et al. 2010). Striking seasonal changes that occur in boreal systems, as well as cyclical demands of reproduction, strongly influence individual survival. With respect to this variability, we examined seasonal range use of moose grouped by sex and reproductive status. Some findings were potentially confounded by small sample size due to low GPS fix rate success, especially for females (66%), which could cause location bias and increase type II error. Corrections for land-cover or terrain characteristics (Frair et al. 2004) or habitat transition probabilities (Nielsen et al. 2009) were not feasible, nor can such corrections

address the geographical space of missing locations (Frair et al. 2010). Nonetheless, few studies have used radio-collared moose to compare habitat use between sexes and by reproductive class (e.g., Oehlers et al. 2011, Bjørneraas et al. 2012, Joly et al. 2015), and despite modest sample sizes, we provide initial insights into seasonal habitat use by moose in south-central Yukon.

Ranges used by moose

Range sizes, particularly in large sexually dimorphic ungulates, vary with body size, landscape heterogeneity, and predictability of resources (Cederlund and Sand 1994, Mysterud et al. 2001, Van Beest et al. 2011). Annual kernel range sizes of moose in this study were similar to those in southeast Alaska

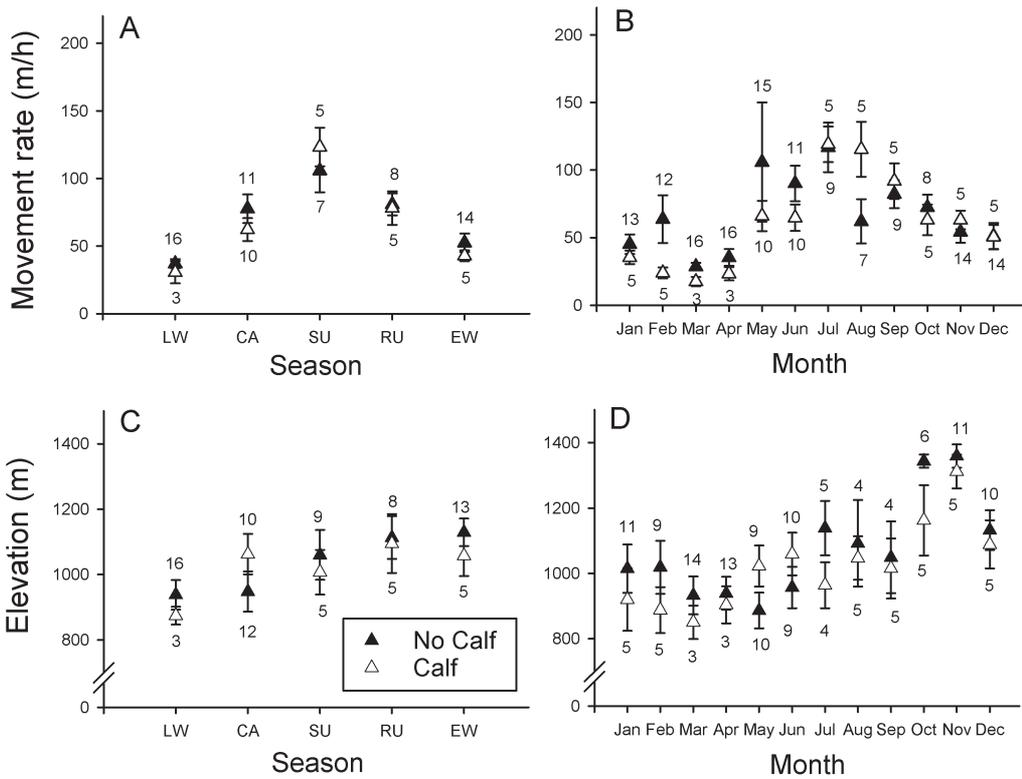


Fig. 3. Average ($\bar{x} \pm SE$) A) seasonal and B) monthly movement rates (m/h), and C) seasonal and D) monthly elevation use by female radio-collared moose with and without calves in the South Canol study area of south-central Yukon, Canada. LW = Late Winter, CA = Calving, SU = Summer, RU = Rut, EW = Early Winter. Numbers shown are sample sizes.

(males and females, Oehlers et al. 2011) and adjacent British Columbia (females, Gillingham and Parker 2008). We also found significant differences in size of seasonal ranges. The large and variable range sizes used by moose during Rut presumably reflected widespread movement and use of a larger portion of the landscape for reproductive purposes. Kernel ranges were smallest in Late Winter when snow depth presumably was greatest and body condition poorest. There was no statistical difference between the size of male and female ranges, and calf presence did not affect range size of females. It is possible that sexual differences occurred at a scale finer than 25-m resolution in terms of resource use and availability. Nonetheless, examining apparent trends in seasonal use patterns among males and females (with and without calves)

can be informative. Male moose, perhaps able to travel more freely than females during the growing seasons, tended to have larger home ranges than females during Calving, Summer, and Rut. Larger males, unhindered by the presence of a calf, can be less selective about forage quality (Ruckstuhl 1998, Barboza and Bowyer 2000). Females are smaller and consequently less energy-constrained than males during winter, but face highest energetic demands during Calving and Summer (White and Berger 2001). Females with calves tended to have smaller ranges than females without calves during Calving.

We used both minimum convex polygons (MCP) and kernel density estimates to calculate range sizes. MCPs, as the area where all use locations were recorded, are more easily compared with other studies.

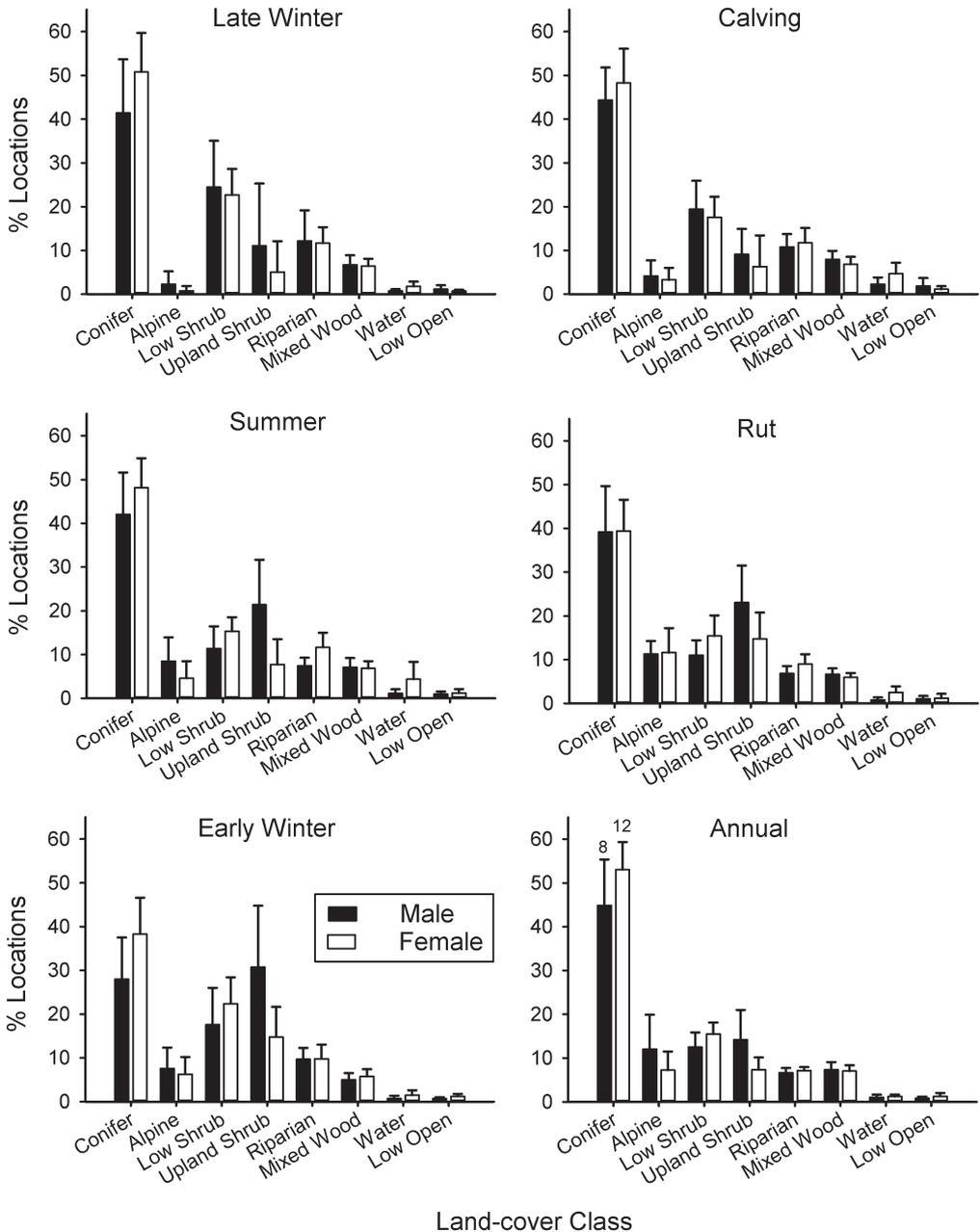


Fig. 4. Seasonal and annual use (% of locations, $\bar{x} \pm SE$) of 8 land-cover classes by male and female radio-collared moose in the South Canol study area of south-central Yukon, Canada.

Fixed kernels, on the other hand, highlight areas that are used most consistently, but different contour values and smoothing factors can make comparison among studies difficult. Fixed kernel values for seasonal ranges were between 13% and 35% of the size of

areas calculated with MCPs in our study. This proportion declined during Summer and Rut for ranges of males, but increased for ranges of females. The difference in the percent metrics of home range size between sexes may indicate that males travel over

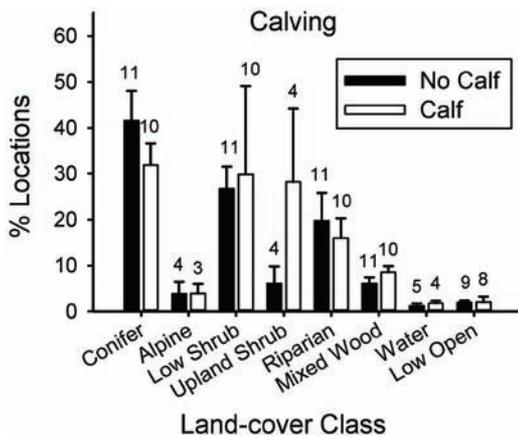


Fig. 5. Use (% of locations, $\bar{x} \pm SE$) of 8 land-cover classes by female radio-collared moose with and without calves during the calving season in the South Canol study area of south-central Yukon, Canada. Numbers shown are sample sizes.

larger areas during Summer and Rut, but favour smaller key areas within that range to meet specific requirements (e.g., mating, feeding). Female moose, in contrast, may target prime habitats initially, and therefore, may not need to be as selective afterward.

Movements of moose

Seasonal movement rates by moose observed in our study reflected changing physiological needs (e.g., rut, parturition) and environmental cycles (e.g., green-up, snow conditions). Because of differences in reproductive demands and body size, movement rates may differ among sex and age groups (Testa et al. 2000). Coady (1974) reported that winter movement rates were most influenced by the relative ability of individual moose to move in deep snow. Similarly, the movement rates of both sexes of moose in the South Canol area were lowest in Late Winter, followed by an increase in movement rates corresponding with rapid snowmelt that typically occurs in May. Movement rates generally increased as the growing season progressed, peaking in July for females

and September for males; rates then gradually declined as winter progressed. This pattern of rapid movement onto summer ranges and gradual movement onto winter ranges has been observed by others (Coady 1974, Vander Wal and Rodgers 2009). A similar pattern of seasonal and monthly movement rates of female moose was observed in northern British Columbia, with comparable climatic conditions and population densities of moose (Gillingham and Parker 2008). Relative to differences in reproductive demands, Joly et al. (2015) documented substantive increases in weekly movement rates of Alaskan male moose in fall, corresponding to the onset of rut and hunting pressures. McGraw et al. (2014) used 20-min locations to monitor long-distance pre-parturition movements of female moose in Minnesota.

High individual variation restricted our ability to detect significant differences in movement rates between male and female moose. We expected different movement rates based on different energetic demands and the reproductive roles faced by each sex. Although statistically insignificant with our small sample size, the greatest potential differences tended to be during Calving and Rut, particularly in June, September, and October when the reproductive roles of males and females are most distinct. During the Calving season prior to birth, females may reduce predation risk by making unusual movements (Bowyer et al. 1999, McGraw et al. 2014); post-parturition movements are limited by newborn calves with limited mobility during their first month. During Rut, males are preoccupied with finding mates and/or defending one or more females from rivals. To successfully reproduce, males may travel long distances or make frequent movements while interacting with mates or rivals (Ballard et al. 1991, Leblond et al. 2010).

Movement rates of females with and without calves were more similar than

between the sexes. When calves become more mobile, females may move frequently as a way to reduce predation risk (Testa et al. 2000), as suggested by our data. Frequent movements may be necessary to access sufficient high-quality forage required to support the energetic demands of feeding and defending a calf. The high variation among females without calves during the Calving season could have been confounded by misclassification during the aerial calf-survival surveys. For example, females that lost a calf prior to the surveys in mid-June, 3 weeks after peak calving in Yukon (Miquelle et al. 1992), would have been classified as females without calves. Bowyer et al. (1999) found that 78% of calves in Denali National Park, Alaska were killed by predators in the first 20 days of life.

Elevations used by moose

Land cover, snow depth, and predation risk may change along altitudinal gradients (Kunkel and Pletcher 2000, Stumph and Wright 2007). In the South Canol area, moose were generally found within a 500-m elevational range from valley bottoms to subalpine areas where elevation may act as a proxy for interpreting response to snow depth. Moose in other areas descend in elevation in response to increasing snow depth (Poole and Stuart-Smith 2006). Indeed, both sexes used lower elevations in Late Winter and Calving and highest elevations during Rut and Early Winter, peaking in November. Moose gradually descended until the end of Late Winter, coinciding with the gradual accumulation of snow over the course of winter.

Female moose use a variety of strategies to select birth sites, reflective of differences in behaviour relative to predator avoidance. Alaskan moose gave birth at higher elevations where predators were less abundant (Bowyer et al. 1999), whereas females in British Columbia appeared to associate with

either of 2 elevational strategies to reduce predation risk: climbers or non-climbers (Poole et al. 2007). We found no differential elevation use between males and females, nor among females with and without calves. We expected elevation use by both sexes to be most similar during Rut, and found the least amount of variation in October and November. Both sexes also used similar elevations during the Calving season, presumably in response to initial vegetation green-up in June. As Summer progresses, so too does the elevational gradient of green-up (Hebblewhite et al. 2008), and likewise, moose in the South Canol area ascended in elevation during Summer and again in Rut. The high variation among individuals during Summer and after the post-rut period may reflect a variety of strategies employed by individuals to maximize energy intake while managing predation risk, or simply reflect a similar strategy employed under variable conditions experienced by individual moose. Similar seasonal patterns were observed in northern British Columbia (Gillingham and Parker 2008).

Land-cover classes used by moose

Moose modify their foraging behavior in response to seasonal changes (Saether and Andersen 1990), and we found seasonal differences in use of 6 of 8 land-cover classes in the South Canol area. In Late Winter, moose were less often in the higher elevation land-cover classes (i.e., Alpine, Upland Shrub) than during Summer, Rut, or Early Winter, suggesting again, that snow depth is a limiting factor for moose in south-central Yukon. Lowland Shrub was used more often in Late Winter than in other seasons, and in addition to lower snow depth, this habitat provides an important forage base presumably key to winter survival. Moose also used less Alpine and Upland Shrub during the Calving season than at other times of the year. As such, they remained in areas with higher availability of

forage in spring to recover from energetic losses of the previous winter. We expected females to minimize predation risk to newborn calves by using more cover during the Calving season, and females with calves tended to use both Upland and Lowland Shrub which provided optimal forage resources and likely reduced predation risk. During Summer, moose continued to use Conifer cover at levels similar to Calving, which in addition to reducing exposure of young calves to predation risk, may be important in moderating extremes of heat. Moose were more likely to encounter Alpine areas as they ascended in elevation during the growing season.

Highest nutritional demands occur during lactation, rearing of young, and fat storage (Belovsky and Jordan 1978), and moose consume 3–4 x more food in summer than winter (Renecker and Hudson 1985). Therefore, we assumed that moose would use shrub-dominated land-cover classes more often during the growing season. Surprisingly, they used shrub classes proportionally less than during Early or Late Winter. This observation highlights both the ability of moose to use a wide variety of stand cover types and age classes to meet their nutritional requirements in Summer when food is plentiful, as well as the importance of accessible shrub-dominated land-cover during winter when snow depth may limit mobility and access to forage. In Early Winter, moose maximized their use of Upland Shrub while reducing use of Conifer. These patterns and corresponding use of higher elevations support our contention that moose generally ascend during Summer and Rut, and remain until snow depth eventually forces them lower in winter. Local knowledge, which adds an additional long-term perspective to this study (McLeod and Clarke 2011), contends that moose typically remain in small groups in subalpine areas after Rut until snow depth

forces them to lower elevations. It is unclear, however, why these subalpine areas are selectively used at that time of year.

Use of Riparian areas and Water by moose in the South Canol area remained fairly constant over the year. Widespread distribution of water bodies in the study area reduced the likelihood of water being a limiting factor. During the Calving season, however, the Water land-cover class was used more often than the annual average, suggesting that access to water may influence habitat use during this season. Local knowledge (McLeod and Clarke 2011) further suggests that access to water is a primary component of birth-site selection. Females have higher water demands during lactation, and movements with a newborn calf are restricted for the first few weeks post-birth (Testa et al. 2000).

Thus, habitat use information combined with resource selection strategies for the same animals (McCulley et al. 2017a) suggest that forage is the driving force in moose ecology in the South Canol area. In almost all seasons, moose demonstrated relatively high use and positive selection for shrub-dominated classes such as Upland or Lowland Shrub and Riparian. Opposing use and selection trends can indicate that resource decisions are made at different scales. For example, in contrast with the use data, selection models indicated that Conifer land cover was avoided (negative selection coefficient). The high use of Conifer presumably occurred because it was so widespread on the boreal landscape (45% of the study area, Table 1), and thus is important at a broad scale. At the smaller scale of seasonal home ranges, moose selected against conifer stands in favour of land-cover classes assumed to have better forage availability (e.g., Lowland Shrub). In contrast, if a resource is selected (as indicated by a positive selection coefficient) and use is low (as per telemetry locations), that resource is probably relatively rare at that scale.

In this study, we demonstrated seasonal differences in range sizes, movement rates, and use of elevation and land cover by moose in south-central Yukon. These differences presumably reflected the responses of individuals to changing resource availability that is characteristic of northern boreal forests. The space-use patterns and movements presented here are driven by selection strategies related to accessing forage and cover, while minimizing predation and harvest risk, within environmental constraints (McCulley et al. 2017a). Taken together, these 2 studies provide complementary information for resource managers towards understanding the potential effects of anthropogenic land use or climate change on moose populations in south-central Yukon.

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REFERENCES

- ADDISON, R. B., J. C. WILLIAMSON, B. P. SAUNDERS, and D. FRASER. 1980. Radio-tracking of moose in the boreal forest of northwestern Ontario. *Canadian Field-Naturalist* 94: 269–276.
- ANDERSEN, R., and B.-E. SAETHER. 1992. Interactions between a generalist herbivore, the moose, and its winter food resources: a study of behavioural variation. *Alces Supplement 1*: 101–104.
- ARTHUR, S. M., B. F. J. MANLY, L. L. McDONALD, and G. W. GARNER. 1996. Assessing habitat selection when availability changes. *Ecology* 77: 215–227.
- BALLARD, W. B. 1992. Bear predation on moose: a review of recent North American studies and their management implications. *Alces Supplement 1*: 162–176.
- , J. S. WHITMAN, and D. J. REED. 1991. Population dynamics of moose in south-central Alaska. *Wildlife Monographs* 114: 5–49.
- BALSOM, S., W. B. BALLARD, and H. A. WHITLAW. 1996. Mature coniferous forest as critical moose habitat. *Alces* 32: 131–140.
- BARBOZA, P. S., and R. T. BOWYER. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy* 81: 473–489.
- BELOVSKY, G. E. 1981. A possible population response of moose to sodium availability. *Journal of Mammalogy* 62: 631–633.
- , and P. A. JORDAN. 1978. The time-energy budget of a moose. *Theoretical Population Biology* 14: 76–104.
- , and ———. 1981. Sodium dynamics and adaptations of a moose population. *Journal of Mammalogy* 62: 613–621.
- BJØRNERAAS, K., I. HERFINDAL, E. J. SOLBERG, B.-E. SAETHER, B. VAN MOORTER, and C. M. ROLANDSEN. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia* 168: 231–243.
- BOWYER, R. T., V. VAN BALLEMBERGHE, J. G. KIE, and J. A. MAIER. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy* 80: 1070–1083.

- BUBENIK, A. B. 2007. Evolution, taxonomy and morphology. Pages 77–123 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. 2nd Edition. University Press of Colorado, Boulder, Colorado, USA.
- BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24: 346–352.
- CEDERLUND, G., and H. SAND. 1994. Home-range size in relation to age and sex in moose. *Journal of Mammalogy* 75: 1005–1012.
- COADY, J. W. 1974. Influence of snow on behaviour of moose. *Naturaliste Canadien* 101: 417–436.
- CONRADT, L., T. H. CLUTTON-BROCK, and F. E. GUINNESS. 2000. Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behaviour* 59: 1049–1060.
- COURTOIS, R., and A. BEAUMONT. 1999. The influence of accessibility on moose hunting in northwestern Quebec. *Alces* 35: 41–50.
- CRICHTON, V., T. BARKER, and D. SCHINDLER. 2004. Response of a wintering moose population to access management and no hunting – a Manitoba experiment. *Alces* 40: 87–94.
- DUNGAN, J. D., and R. G. WRIGHT. 2005. Summer diet composition of moose in Rocky Mountain National Park, Colorado. *Alces* 41: 139–146.
- DUNNETT, C. W., and M. GENT. 1977. Significance testing to establish equivalence between treatments with special reference to data in the form of 2x2 tables. *Biometrics* 33: 593–602.
- DUSSAULT, C., R. COURTOIS, J.-P. OUELLET, and I. GIRARD. 2005a. Space use of moose in relation to food availability. *Canadian Journal of Zoology* 83: 1431–1437.
- , ———, ———, and J. HUOT. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. *Wildlife Society Bulletin* 29: 171–179.
- , J.-P. OUELLET, R. COURTOIS, J. HUOT, L. BRETON, and H. JOLICOEUR. 2005b. Linking moose habitat selection to limiting factors. *Ecography* 28: 619–628.
- ESRI 2006. ArcMap GIS, Release 9. Environmental Systems Research Institute, Redlands, California.
- FLORKIEWICZ, R., J. McLELLAND, S. WESTOVER, and R. WARD. 2008. Summary of the South Canol West early-winter 2007 moose survey. Yukon Department of Environment (unpublished report). Whitehorse, Yukon, Canada.
- FORMAN, R. T., and L. E. ALEXANDER. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207–231.
- FRAIR, J. L., S. E. NIELSEN, E. H. MERRILL, S. R. LELE, M. S. BOYCE, R. H. MUNRO, and H. BEYER. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41: 201–212.
- , J. FIEBERG, M. HEBBLEWHITE, F. CAGNACCI, N. J. DECESARE, and L. PEDROTTI. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2187–2200.
- FRASER, D., B. K. THOMPSON, and D. ARTHUR. 1982. Aquatic feeding by moose: seasonal variation in relation to plant chemical composition and use of mineral licks. *Canadian Journal of Zoology* 60: 3121–3126.
- GILLINGHAM, M. P., and K. L. PARKER. 2008. Differential habitat selection by moose and elk in the Besa-Prophet area of northern British Columbia. *Alces* 44: 41–63.
- HAYES, R. D., A. M. BAER, U. WOTSCHIKOWSKY, and A. S. HARESTAD. 2000. Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology* 78: 49–59.
- , and A. S. HARESTAD. 2000. Wolf functional response and regulation of moose in the Yukon. *Canadian Journal of Zoology* 78: 60–66.

- HEBBLEWHITE, M., E. MERRILL, and G. McDERMID. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78: 141–166.
- JAMES, A. R. C., and A. K. STUART-SMITH. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64: 154–159.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- JOLY, K., T. CRAIG, M. S. SORUM, J. S. McMILLAN, and M. A. SPINDLER. 2015. Variation in fine-scale movements of moose in the upper Koyukuk River drainage, northcentral Alaska. *Alces* 51: 97–105.
- KUNKEL, K. E., and D. H. PLETCHER. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78: 150–157.
- LARSEN, D. G., D. A. GAUTHIER, and R. L. MARKEL. 1989. Causes and rate of moose mortality in the southwest Yukon. *Journal of Wildlife Management* 53: 548–557.
- LEBLOND, M., C. DUSSAULT, and J.-P. OUELLET. 2010. What drives fine - scale movements of large herbivores? A case study using moose. *Ecography* 33: 1102–1112.
- MABILLE, G., C. DUSSAULT, J.-P. OUELLET, and C. LAURIAN. 2012. Linking trade-offs in habitat selection with the occurrence of functional responses for moose living in two nearby study areas. *Oecologia* 170: 965–977.
- MAIER, J. A. K., J. M. VERHOEF, A. D. MCGUIRE, R. T. BOWYER, L. SAPERSTEIN, and H. A. MAIER. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. *Canadian Journal of Forest Research* 35: 2233–2243.
- MAIN, M. B., and B. E. COBLENTZ. 1990. Sexual segregation among ungulates: a critique. *Wildlife Society Bulletin* 18: 204–210.
- , F. W. WECKERLY, and V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* 77: 449–461.
- MANSSON, J., H. ANDREN, A. PEHRSON, and R. BERGSTROM. 2007. Moose browsing and forage availability: a scale-dependent relationship? *Canadian Journal of Zoology* 85:372–380.
- MAUER, F. J. 1998. Moose migration: north-eastern Alaska to northwestern Yukon Territory, Canada. *Alces* 34: 75–81.
- MCCULLEY, A. M. 2015. Habitat use and selection by male and female moose (*Alces alces*) in a boreal landscape. M. Sc. Thesis. University of Northern British Columbia, Prince George, British Columbia, Canada.
- , K. L. PARKER, and M. P. GILLINGHAM. 2017a. Yukon moose: I. Seasonal resource selection by males and females in a multi-predator boreal ecosystem. *Alces* 53: 113–136.
- MCGRAW, A. M., J. TERRY, and R. MOEN. 2014. Pre-parturition movement patterns and birth site characteristics of moose in northeast Minnesota. *Alces* 50: 93–104.
- MCLELLAN, B. N., and D. M. SHACKLETON. 1988. Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. *Journal of Applied Ecology* 25: 451–460.
- MCLEOD, T. P., and H. D. M. CLARKE. 2011. Local knowledge-based moose habitat suitability assessment – South Canol region, Yukon. Yukon Fish and Wildlife Branch Draft Report, Whitehorse, Yukon, Canada.
- MIQUELLE, D. G., and P. A. JORDAN. 1979. The importance of diversity in the diet of moose. *Proceedings of the North American Moose Conference Workshop* 15: 54–79.
- , J. M. PEEK, and V. Van BALLEMBERGHE. 1992. Sexual segregation in Alaskan moose. *Wildlife Monographs* 122: 1–57.

- MITCHELL, M. S., and R. A. POWELL. 2012. Foraging optimally for home ranges. *Journal of Mammalogy* 93: 917–928.
- MYSTERUD, A., and E. OSTBYE. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Society Bulletin* 27: 385–394.
- , R. LANGVATN, N. G. YOCOZ, and N. CHR. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* 70: 915–923.
- NIELSON, R. M., B. F. J. MANLY, L. L. McDONALD, H. SAWYER, and T. L. McDONALD. 2009. Estimating habitat selection when GPS fix success is less than 100%. *Ecology* 90: 2956–2962.
- OEHLERS, S. A., R. T. BOWYER, F. HUETTMANN, D. K. PERSON, and W. B. KESSLER. 2011. Sex and scale: implications for habitat selection by Alaskan moose *Alces alces gigas*. *Wildlife Biology* 17: 67–84.
- OSKO, T. J., M. N. HILTZ, R. J. HUDSON, and S. M. WASEL. 2004. Moose habitat preferences in response to changing availability. *Journal of Wildlife Management* 68: 576–584.
- PCI GEOMATICS. 2009. Geomatica, Release 10.3. Richmond Hill, Ontario, Canada.
- PHILLIPS, R. L., W. E. BERG, and D. B. SINIFF. 1973. Moose movement patterns and range use in northwestern Minnesota. *Journal of Wildlife Management* 37: 266–278.
- POOLE, K. G., and K. STUART-SMITH. 2006. Winter habitat selection by female moose in western interior montane forests. *Canadian Journal of Zoology* 84: 1823–1832.
- , R. SERROUYA, and K. STUART-SMITH. 2007. Moose calving strategies in interior montane ecosystems. *Journal of Mammalogy* 88: 139–150.
- POWELL, R. A., and M. S. MITCHELL. 2012. What is a home range? *Journal of Mammalogy* 93: 948–958.
- RENECKER, L. A., and R. J. HUDSON. 1985. Estimation of dry-matter intake of free-ranging moose. *Journal of Wildlife Management* 49: 785–792.
- , and ———. 1992. Thermoregulatory and behavioural response of moose: is large body size an adaptation or constraint? *Alces Supplement* 1: 52–64.
- , and C. C. SCHWARTZ. 2007. Food habits and feeding behaviour. Pages 403–439 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. 2nd Edition. University Press of Colorado, Boulder, Colorado, USA.
- RUCKSTUHL, K. E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour* 56: 99–106.
- SAETHER, B.-E., and R. ANDERSEN. 1990. Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constraints on behavioural decisions. *Canadian Journal of Zoology* 68: 993–999.
- SCHWARTZ, C. C., and L. A. RENECKER. 2007. Nutrition and energetics. Pages 441–478 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. 2nd Edition. University Press of Colorado, Boulder, Colorado, USA.
- SIGNER, J., N. BALKENHOL, M. DITMER, and J. FIEBERG. 2015. Does estimator choice influence our ability to detect changes in home-range size? *Animal Biotelemetry* 3: 16–24.
- STATA CORP. 2011. Stata Statistical Software, Release 12. StataCorp LP, College Station, Texas, USA.
- STUMPH, B. P., and R. G. WRIGHT. 2007. Effects of willow quality on moose distribution in a montane environment. *Alces* 43: 129–142.
- TELFER, E. S. 1970. Winter habitat selection by moose and white-tailed deer. *Journal of Wildlife Management* 34: 553–559.
- . 1984. Circumpolar distribution and habitat requirements of moose

- (*Alces alces*). Pages 145–182 in R. Olsen, R. Hastings, and F. Geddes, editors. Northern Ecology and Resource Management. University of Alberta Press, Edmonton, Alberta, Canada.
- TESTA, J. W., E. F. BECKER, G. R. LEE, W. B. BALLARD, and A. R. RODGERS. 2000. Movements of female moose in relation to birth and death of calves. *Alces* 36: 155–162.
- TIMMERMANN, H. R., and J. G. McNICOL. 1988. Moose habitat needs. *Forestry Chronicle* 64: 238–245.
- TROMBULAK, S. C., and C. A. FRISSELL. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18–30.
- VAN BALLEMBERGHE, V., and J. M. PEEK. 1971. Radiotelemetry studies of moose in northeastern Minnesota. *Journal of Wildlife Management* 35: 63–71.
- , D. G. MIQUELLE, and J. G. MACCRACKEN. 1989. Heavy utilization of woody plants by moose during summer at Denali National Park, Alaska. *Alces* 25: 31–35.
- VAN BEEST, F. M., I. M. RIVRUD, L. E. LOE, J. M. MILNER, and A. MYSTERUD. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology* 80: 771–785.
- VANDER WAL, E., and A. R. RODGERS. 2009. Designating seasonality using rate of movement. *Journal of Wildlife Management* 73: 1189–1196.
- WHITE, K. S., and J. BERGER. 2001. Anti-predator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? *Canadian Journal of Zoology* 79: 2055–2062.
- WULDER, M. A., J. A. DECHKA, M. A. GILLIS, J. E. LUTHER, R. J. HALL, A. BEAUDOIN, and S. E. FRANKLIN. 2003. Operational mapping of the land cover of the forested area of Canada with Landsat data: EOSD land cover program. *Forestry Chronicle* 79: 1075–1083.
- YUKON ECOREGIONS WORKING GROUP. 2004. Pelly Mountains. Pages 219–226 in C. A. S. Smith, J. C. Meikle, and C. F. Roots, editors. Ecoregions of the Yukon Territory: Biophysical Properties of Yukon Landscapes. PARC Technical Bulletin No. 04-01. Agriculture and Agri-Food Canada, Summerland, British Columbia, Canada.