THE SEASONALITY OF A MIGRATORY MOOSE POPULATION IN NORTHERN YUKON

Dorothy Cooley[1,5], Heather Clarke[1], Shel Graupe[2,6], Manuelle Landry-Cuerrier[3], Trevor Lantz[4], Heather Milligan[1], Troy Pretzlaw[3,7], Guillaume Larocque[3,8], and Murray M. Humphries[3]

[1]Department of Environment, Yukon Government, Whitehorse, YT, Canada, Y1A 2C6; [2]Vuntut Gwitchin Government, Old Crow, YT, Canada, Y0B 1N0; [3]Natural Resource Sciences, Macdonald Campus, McGill University, Ste-Anne-de-Bellevue, QC, Canada H9X 3V9; [4]Environmental Studies, University of Victoria, Victoria, BC, Canada, V8W 2Y2; [5]Teslin Tlingit Council, Teslin, YT, Canada, YOA 1B0; [6]SGS Canada Inc, Edmonton, AB, Canada, T6E 4N1; [7]Parks Canada, Annapolis, NS, Canada, B0T 1B0; [8]Québec Centre for Biodiversity Science, Montréal, QC, Canada, H3A 1B1

ABSTRACT: At the northern edge of their North American range, moose (*Alces alces*) occupy treeline and shrub tundra environments characterized by extreme seasonality. Here we describe aspects of the seasonal ecology of a northern Yukon moose population that summers in Old Crow Flats, a thermokarst wetland complex, and winters in surrounding alpine habitat. We collared 19 moose (10 adult males and 9 adult females) fitted with GPS radio-collars in Old Crow Flats during summer, and monitored their year-round habitat use, associated environmental conditions, and movements for 2 years. Seventeen of 19 moose were classified as migratory, leaving Old Crow Flats between August and November and returning in April to July, and spent winter in alpine habitats either northwest (n = 8), west (n = 4), or southeast (n = 5) of Old Crow Flats. The straight-line migration distance between summer and winter ranges ranged from 59 to 144 km, averaging 27 km further for bulls than cows. In summer, 18 of 19 moose situated their home ranges in and around drained lake basins and shallow lake habitats within Old Crow Flats. In winter, moose at elevations < 400 m selected for river, shrub, or drained lake habitats, whereas those at elevations >600 m selected for shrubby valley bottoms near lakes and rivers within home ranges dominated by alpine tundra. Moose at high elevations marginally reduced their exposure to cold extremes due to the prevalence of thermal inversions, but cold avoidance was not a strong driver of habitat selection, including for moose at low elevations. Stable isotope signatures of moose hair, aquatic plants, and terrestrial plants were consistent with a year-round, shrub-dominated diet characterized by slight habitat- and season-associated dietary differences. Local knowledge of the Vuntut Gwitchin First Nation predicted several of our major results, including 1) summer home range fidelity, 2) selection of lakeshore habitats, 3) use of drained lake basins, 4) dietary reliance on shrubs and emergent vegetation, and 5) responses to contemporary environmental changes. Although the core habitat of this moose population, including the winter ranges of its 3 subpopulations, is well protected by a variety of special management units, parks, and protected areas in Yukon and Alaska, pronounced climate warming is dramatically impacting this thermokarst wetland. Coordinated monitoring, management, and conservation of this unique landscape, moose population, and socio-ecological system is warranted.

ALCES VOL. 55: 105–130 (2019)

Key words: Alaska-Yukon, alpine, Cervidae, habitat selection, migration, seasonality, subsistence, thermal ecology, traditional ecological knowledge, winter

---

Moose (*Alces alces*) are broadly distributed across the boreal forests of North America and Scandinavia (Telfer 1984), but much recent research has focused on populations at the periphery of their range beyond or at the margins of the boreal forest. At the southern edge of the North American range, a recent period of recolonization and range expansion (Wattles and DeStefano 2011) appears to be transitioning into population decline in certain areas due to impacts of climate change, disease, parasites, and human harvest (Lenarz et al. 2009, van Beest et al. 2012, DeCesare et al. 2015, Monteith et al. 2015, Jones et al. 2019). Conversely, certain populations at the northern edge are expanding range and increasing in abundance at the forest-tundra transition zone (Hayes and Barichello 1986, Jung et al. 2009, Wald and Nielson 2014). Less is understood about habitat and climate conditions that constrain seasonal distribution of forest-tundra moose populations (Tape et al. 2016), specifically, the ecological determinants of their northern range limit in North America.

Moose inhabit highly seasonal environments throughout their range and are generally well-adapted to endure highly seasonal environments. For example, in summer they use aquatic habitats extensively for foraging, cooling, and insect relief (Timmermann and McNicol 1988), whereas in winter their large size counteracts deep snow (Telfer and Kelsall 1984) and cold temperatures (Renecker and Hudson 1986). Seasonal extremes can potentially impact moose populations, particularly as climate change increases summer and autumnal ambient temperature (T_a); e.g., increasing summer T_a influences habitat selection in Norway (van Beest et al. 2012) and longer, warmer autumns increase parasitic infestations in the northeastern United States (Jones et al. 2019). At the northern edge of the range, the duration and severity of winters, the brevity and intensity of summers, and the overall magnitude of seasonal environmental variation presumably influence seasonal movement patterns and habitat use and preferences.

Although most moose populations are not migratory, localized movements between summer and winter ranges are common (Timmermann and McNicol 1988). If seasonal habitat use includes changes in elevation, moose typically occupy lowest elevations in late winter and higher elevations in summer, autumn, and early winter (Hauge and Keith 1981, Jenkins and Wright 1987). Home ranges might be expected to be smaller in summer and larger in winter given that the quantity and quality of forage is higher in summer than winter (Timmermann and McNicol 1988), and home range typically increases as habitat quality declines (van Beest et al. 2011, Bjørneraas et al. 2012). However, snow depth >60 cm impedes movement (Renecker and Schwartz 1998) and restricts winter home range size (Houston 1968, Loisa and Pulliainen 1968, Phillips et al. 1973), with size declining from early to late winter as snow accumulates (Goddard 1970, Van Ballenberghe and Peek 1971, Phillips et al. 1973, Thompson and Vukelich 1981).

Seasonal shifts in habitat use and movements of certain populations are consistent and long enough to be classified as migration (LeResche 1974, Pulliainen 1974, Van Ballenberghe 1977, Mauer 1998, Demarchi 2003, White et al. 2014, Singh et al. 2016, Rolandsen et al. 2017), ranging from < 25 km (Ball et al. 2001) to >150 km (Mauer 1998). The timing of migration varies by population, but typically occurs in late summer and early fall prior to the breeding period, with return around spring thaw. For example, fall migration preceded breeding and was unrelated to snow depth in Alaska (Gasaway et al. 1983), while spring migration occurred after snow depth dissipated to < 16 cm in Sweden (Ball et al. 1999).

Old Crow Flats (Van Tat) is an expansive wetland complex located north of the Arctic Circle in northern Yukon and is important, traditional territory of the Vuntut Gwitchin (People of the Lakes) living in Old Crow. Likewise, moose are an important traditional food for the Vuntut Gwitchin

(Schuster et al. 2011), but are harvested infrequently in Old Crow Flats because they are common there only in summer (Mossop 1975) and seldom encountered during the autumn, winter, and spring harvesting seasons. This seasonal habitat use is described by local traditional knowledge:

> "In the spring it's known from way back [long ago] that moose, they start from the higher ground and go toward the river [and Old Crow Flats]. But during the winter, they stay up in the hills and creeks in the mountains." (Vuntut Gwitchin First Nation and Smith 2010: 215).

Consistent with this observation, moose radio-collared in late winter in the eastern portion of the Brooks Range, Alaska spent summer in the western portion of Old Crow Flats (Mauer 1998). Further, during spring and summer, moose in Old Crow Flats feed on vegetation in the drained margins of lakes:

> "[The best places to hunt moose were] around where you call a dry lake, around the lakes. In summertime, even in wintertime, they stay in one place. They have a trail to where they feed around the lake. You see the grass" (Vuntun Gwitchin First Nation and Smith 2010: 71).

Yeendoo Nanh Nakhweenjit K'atr'ahanahtyaa (YNNK; Taking Care of the Land for the Future) was a community-initiated and community-led International Polar Year project motivated by local observations of rapid landscape change in Old Crow Flats, including warmer temperatures, low water levels, lake drainages, and increased shrub growth (Technical Working Group and the Management Committee [TWGMC] 2006, Wolfe et al. 2011). Major findings of this collaborative research project were that 1) Old Crow Flats is warmer now than at any time in the past 300 years (Porter and Pisaric 2011), 2) catastrophic lake drainages were 4–5 × more frequent from 1972–1990 and 1991–2009 than from 1951–1972 (Lantz and Turner 2015), 3) shoreline stability is compromised by high water level, wave action, ice push, and the presence of ice wedges (Roy-Léveillée and Burn 2010), 4) vegetative cover surrounding lakes determines whether hydrological processes are dominated by snowmelt or rainfall (Turner et al. 2014) which in turn determines lake productivity and other limnological characteristics (Balasubramaniam et al. 2015), and 5) shrub succession in drained basins is proceeding along 2 major trajectories dictated by moisture level (Lantz 2017).

Here we report the findings of moose research conducted as part of the YNNK projexct. We combined local knowledge with that data obtained from GPS radio-collars to describe moose movements and habitat use in Old Crow Flats relative to season, ecosystem change, subsistence use, and habitat protection. From local knowledge, we hypothesized that this moose population would be migratory and express seasonally divergent habitat selection. We predicted that moose in summer would select highly productive, low elevation wetlands within Old Crow Flats, where they would use and prefer early succession, shrubby habitats within and around drained lake basins. In winter, we predicted moose would select shrubby alpine habitats and, due to the prevalence of thermal inversions, these higher elevation habitats would be characterized by warmer air temperatures than lower elevations in Old Crow Flats. Given local knowledge that moose are common in Old Crow Flats in summer but not winter, we radio-collared moose in mid-summer, and tracked the consistency, timing, and spatial extent of movements from Old Crow Flats to determine the location and habitat characteristics of winter ranges.

Seasonality in movement patterns and habitat selection are likely to be key features of moose ecology at the northern range edge, given the magnitude of seasonal variation and its broad effects on resources, predators, thermal stress, and landscape movement. This research was designed to expand the limited knowledge concerning migration and the seasonal ecology of populations at the northern edge of moose range, while considering habitat protection, harvest vulnerability, and climate change sensitivity of a culturally-important Northern Yukon moose population.

STUDY AREA

Old Crow Flats is a 6,170 km^2 wetland complex of international significance (Ramsar Convention 2004) comprised of 40% water (Russell et al. 1978) and containing ~9,000 shallow lakes (Turner et al. 2010, Lantz and Turner 2015) situated within a low elevation basin (<300 m asl) surrounded by mountainous uplands. Although above the Arctic Circle in a zone of continuous permafrost (Roy-Léveillée et al. 2014) and spanning the forest-tundra transition zone, Old Crow Flats is a highly productive wetland system (Smith et al. 2004, Mossop 2015). The shallow, flat-bottomed lakes are highly productive (Allenby 1989, Smith et al. 2004) and surrounded by a mixed community of tall and dwarf shrubs and herbaceous vegetation, with conifer woodlands concentrated around rivers and creeks (Turner et al. 2014). Predators of moose region include wolves (*Canis lupus*), grizzly bears (*Ursus arctos horribilis*), and black bears (*Ursus americanus*) (North Yukon Planning Commission 2009).

Drained lake basins resulting from catastrophic drainages and gradual declines in water level are common across Old Crow Flats and range in age from <10 to >11,000 years (Ovenden 1986, Lauriol et al. 2009, Lantz and Turner 2015). Catastrophic drainages result from lakes elevated above and close to incised streams, in combination with unstable shorelines often related to permafrost degradation, ice push, heavy precipitation and/or wave action that can cause lakes to drain rapidly (Lantz and Turner 2015). Vuntut Gwichin observers have reported vegetation changes in Old Crow Flats and note an increase in the number of lakes draining and drying (Wolfe et al. 2011). Drainage events have been detected from aerial photos and satellite imagery (Lantz and Turner 2015) and observed directly during the study period (Wolfe and Turner 2008).

The climate is characterized by long, cold winters (mean January temperature = −31°C) and short, warm summers (mean July temperature = 15°C) with annual precipitation ~257 mm, with 100 mm as snow (Turner et al. 2010). In general, low elevation localities like Old Crow Flats have warmer summers and longer growing seasons than the surrounding mountains which are cooler in summer with longer periods of snow cover. In non-summer months, temperature inversions characterized by warmer air at higher and cooler air at lower elevations are a common feature in most Arctic regions including northern Yukon and the northeast interior of Alaska (Bradley et al. 1992, Bourne et al. 2010).

METHODS

Study animals

Ten male and 9 female (2 with calf) adult moose were captured between 31 July and 4 August 2007 and fitted with GPS radiocollars (GPS 4400MTM, Lotek, Newmarket, Ontario) programmed to record location, collar temperature, and elevation every 4 (n = 3) or 5 h (n = 16). Fourteen collars were recovered from recaptured animals in August 2009; satellite transmissions from the other

5 animals excluded temperature and elevation data (Fig. 1). For collar deployment, moose were first located from a fixed-wing aircraft, then approached and darted from a helicopter. Immobilization was achieved with a mixture of carfentanil and xylazine or medetomidine (Telazol™) and ketamine; naltrexone and Antisedan™ were used as reversal agents. To avoid stress, chase times were limited and averaged just under 3 min. Once safely immobilized, each was blindfolded and provided oxygen; body temperature, heart rate, breathing rate, blood oxygen level, and blood pressure were monitored continuously. Each received a radio-collar and ear tags to provide identification by researchers and hunters. Blood, fecal, and hair samples were collected and body condition was assessed via ultrasound measurement of rump fat; total handling time was typically 14–20 min. After the reversal procedure, each was monitored until regaining consciousness and on its feet, typically <20 min. No capture mortality was documented.

Migration, home range, and habitat selection

The seasonal timing, spatial extent, and directionality of migration was quantified using the net-squared displacement approach of Bunnefeld et al. (2011) as calculated with the adehabitat package (Calenge 2006) for

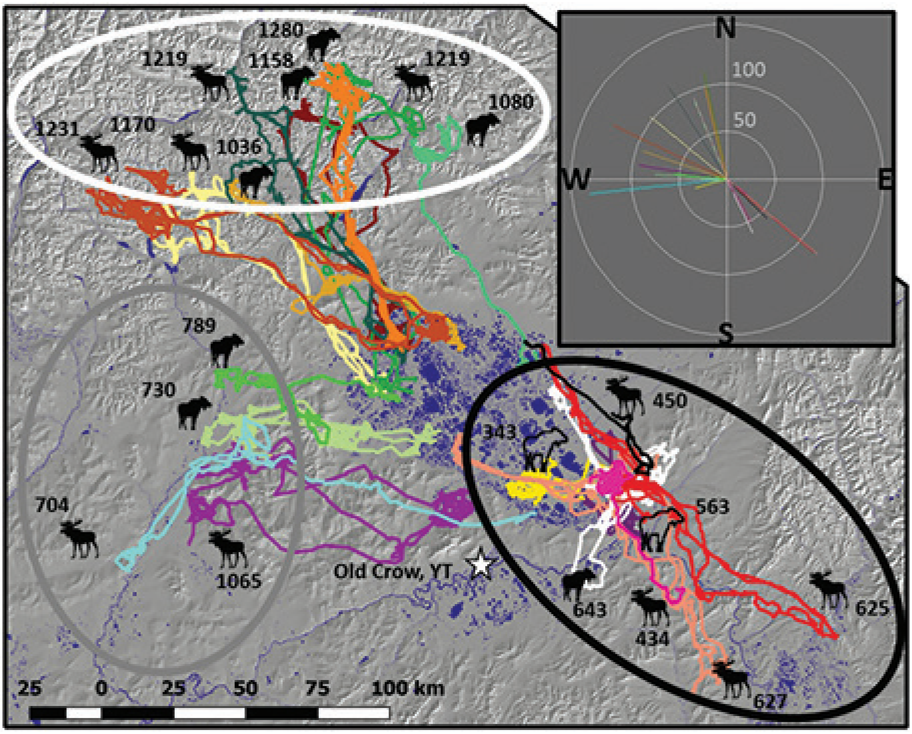

Fig. 1. Individual tracks from GPS radio-collar locations generated from 10 bull and 9 cow moose in Old Crow Flats. The inset panel represents the direction and maximum displacement (km) between summer and winter locations for each moose, including 8 animals that migrated to the northwest (white circle outline), 5 to the west (gray circle outline), and 6 to the southeast (black circle outline), as well as 2 non-migratory cows (outlined icons associated with yellow and dark purple tracks). The maximum elevation (m) used by each moose is indicated next to each icon.

R (R Core Team 2016). This approach examines the linear distance between the first summer location and all subsequent relocations to assess individual trajectory of displacement in space and time. Migratory phases are characterized by progressive changes (sustained increase/decrease over time) in displacement, whereas ranging phases of seasonal residents are characterized by displacement plateaus. Migratory individuals were defined as those exhibiting a plateau-increase and plateau-decrease pattern of displacement over time scales (4 phases summing to 1 year) and distance (> home range diameter) consistent with seasonal migration.

To assess seasonal timing, we defined the start of a migration phase (autumn departure and spring return) for a given individual as the date when its displacement plateau first transitioned into a sustained increase/decrease, and the end of the migration phase as the first date of the plateau. Relocations were classified as ranging after the end of a migration phase (prior to the start of the next phase). To quantify migration distance, we measured the maximum displacement distance between a ranging location in June, July, or August 2007 and a ranging location recorded in December 2007 or January-February 2008. Migration direction was defined as the cardinal direction between these maximally-displaced summer and winter locations. As an alternative measure of migration distance, we also estimated the straight-line distance between the last summer ranging location and the first winter ranging location. We also estimated migratory path lengths as the sum of location-to-location distances from the last summer ranging location to the first winter ranging location; movement rates were based on path lengths travelled per unit time. Finally, the relative straightness of migratory routes was estimated as linear displacement/path length, again based on the last summer and first winter ranging locations.

We estimated seasonal home ranges using single minimum convex hulls in QGIS (QGIS Development Team 2016) with ranging locations recorded in winter 2007–2008 and summer 2008. We focus on these 2 consecutive seasons because they provided the most individuals (the same 7 bulls and 7 cows) with complete data. The average number of locations used to calculate individual home ranges was 376 (range = 128–544) in winter 2007–2008 and 362 (range = 92–551) in summer 2008. The location numbers reflect differences in the pre-set fix rate (3 collars recorded location every 4 h, 11 collars every 5 h), missed fixes (4% average, range = 0–34% in winter 2007–2008; 5% average, range = 0–40% in summer 2008), and certain animals commencing migration during the summer (n = 7) and winter sampling periods (n = 9). We controlled for this source of variation by including the number of locations/season/individual as a covariate in our analysis of gender and seasonal differences in home range size, and calculating home ranges with a standardized number of locations (n = 200) that was intermediate of the minimum and maximum number of locations per individual/season.

To assess habitat use, we aggregated 2 terrain classifications developed for Old Crow Flats (Turner et al. 2014, Lantz and Turner 2015) into a simplified classification extended across a larger spatial area that encompassed the winter range outside Old Crow Flats (Fig. S1). In addition to the land cover classes described in Turner et al. (2014), we included 3 other classes (glacier ice, tussock tundra, and lush vegetation/shrub thicket) frequently found at higher elevations around Old Crow Flats, and a separate class for drained lake basin which is hypothesized as important moose habitat (Lantz and Turner 2015). These land cover classes were combined into 7 aggregated habitat categories (Table S1): forest, lake, river, shrub, tundra, barren, and drained.

We used these habitat categories to assess second-order (home range habitat within study area) and third-order (habitat use within the home range) habitat selection (Johnson 1980) of moose in winter and summer. For second-order selection, we considered the entire study area as the available habitat for all individuals (Design II in Manly et al. 2007). We emphasize this second-order analysis because: 1) given the distances and variable timing of the migration movements we observed, it was reasonable to assume that any individual moose could have moved anywhere in the study area within days or weeks, and 2) this scale of selection relates most directly to our seasonal hypothesis because it compares the habitat characteristics of occupied home ranges to those available if an animal had not migrated, or migrated to a different location. Because the second-order selection is likely complemented by third-order selection of specific habitat features, we considered a 100-m buffer radius around each ranging location as the used habitat and the associated individual home range as the available habitat (Design III in Manly et al. 2007). Using log-likelihood chi-squared statistics in the adehabitat package (Calenge 2006) for R (R Core Team 2016), we computed selection ratios to test whether individuals used habitats in proportion to availability and whether selection was similar for all individuals.

Influence of air temperature

This analysis evaluated the hypothesis that moose capitalize on thermal inversions by moving to higher elevations in winter to avoid cold temperature extremes in Old Crow Flats. Because different moose occupied a range of elevations at any point in time (except in summer), relating collar temperature to elevation provided a means to assess the prevalence and strength of inversions within the study region, and the potential use of elevation in defining the thermal environment occupied by moose. Specifically, we predicted that in winter, i) temperatures recorded by collars (T_c) in winter would be positively correlated with elevation, ii) the relationship between T_c at high elevations and ambient temperature ($\mathrm{T_a}$) at low elevations would be characterized by a breakpoint, below which high elevation T_c would decline less than $\mathrm{T_a}$ at low elevation, iii) if moose demonstrated temperature selection through comparison of used versus available $\mathrm{T_a}$, the strongest selection would occur at high elevation when $\mathrm{T_a}$ was coldest, and iv) moose were more likely to move from low to high elevation when a decline in $\mathrm{T_a}$ coincided with development of a thermal inversion.

Data available during the study were primarily limited to hourly measurements of $\mathrm{T_a}$ at the Old Crow airport (elevation 251 m, hereafter $T_{a\text{-}OC}$) and T_c measured by 14 of the radio-collars. In addition, a temporary weather station positioned within the central portion of Old Crow Flats (67.903995 °N, −139.746503 °W, elevation 308 m) recorded hourly measurements of $\mathrm{T_a}$ from June 2008 to September 2011. Hourly $T_{a\text{-}OC}$ was highly correlated with that measured at the temporary station in Old Crow Flats ($T_{a\text{-}OCF}$) on 5 August 2008 to 2 August 2009 ($r = 0.986$, $n = 8712$, $P < 0.0001$); 88 and 98% of observations differed < 5 and < 10°C, respectively (Fig. S2a). The pattern of residual variation around this correlation indicated that summer temperatures were slightly warmer at Old Crow airport than within Old Crow Flats (e.g., when $T_{a\text{-}OC}$ = 25°C, predicted $T_{a\text{-}OCF}$ = 22.7°C), with winter temperatures more similar (e.g., when $T_{a\text{-}OC}$ = −40°C, predicted $T_{a\text{-}OCF}$ = −41.0°C). The largest deviations that occasionally exceeded 10°C (1.8% of observations) tended to occur in winter when $T_{a\text{-}OC}$ was between −5 and −30°C (Fig. S2b).

We tested prediction i) by assessing the correlation between T_c and elevation from 1 October to 30 April when moose occupied a wide range of elevations (coefficient of variation > 30%). The basis of this comparison was the range of elevations occupied by different animals and the corresponding T_c at a given point in time. We assessed this relationship 6 times per day (T_c was recorded every 4–5 h) using simple linear regression where slope represented the change in T_c by elevation, hereafter defined as L for lapse rate in °C/1000 m; sample size was the number of moose with measured T_c and elevation during the 4–5 h interval. Because L was likely to change over time as thermal inversions form and dissipate (Bradley et al. 1992), we used a generalized additive model (GAM) to assess how L varied over time in relation to time of day (fitted as a cyclic cubic spline function), day of year (also fitted as a cyclic cubic spline function) interacting with elevation (fitted non-isotropically using the "tensor product" smoothing function which performs better when covariates are not on the same scale), and habitat category (fitted as a factor) in the package mgcv (Wood 2017) for R (R Core Team 2016).

We tested prediction ii) by assessing the relationship between T_c recorded on 14 moose and $T_{a\text{-}OC}$. For each we examined the $T_{a\text{-}OC}$ threshold at which the relationship between T_c and $T_{a\text{-}OC}$ decouples by fitting a 2-phase linear regression using the package segmented (Muggeo 2017) for R (R Core Team 2016). We then assessed whether the position and slope of the low temperature divergence was related to the maximum elevation occupied by moose in winter.

We tested prediction iii) by interpreting T_c as the used temperature and comparing it to available $\mathrm{T_a}$s which were estimated using a combination of $T_{a\text{-}OC}$ and the T_c recorded at various elevations. Specifically, T_a at a given elevation e_x, at a given time t_y was estimated with the following equation:

$$= T_{a-OC,t_y} + \left(e_x - e_{OC}\right) L_{t_y}$$

where $T_{a\text{-}OC}$ is the temperature at Old Crow airport, e_{OC} is the elevation of Old Crow airport (251 m), and L_{ty} is the estimated lapse rate at time t_y in units °C/1000 m. We estimated T_a for 42 e_x (25 m increments from 225 to 1250 m) at 6 t_y per day from 3 August 2007 to 5 August 2009. For t_y between 1 October and 30 April, we used the GAM described above to estimate L as the slope of the relationship between T_c and elevation recorded by 14 radio-collars (excluding time blocks with < 3 recordings) using a fixed time and habitat category (i.e., 1200 h in tundra habitat). For t_y between 1 May to 30 September when inversions rarely occur (Bradley et al. 1992), and most moose occupied only low elevations, we adjusted $T_{a\text{-}OC}$ to reflect the average relationship (intercept and slope) with T_c recorded on 3 moose at similar elevations (Table S2), and assumed L was equal to the dry adiabatic lapse rate of −9.8°C/1000 m.

Finally, to test prediction iv), we combined information on the temporal pattern of thermal inversions with moose movements. This included an analysis of individual mid-day movements as a function of T_c, using the minimum distance (m) moved during the same 4- or 5-hour period ending between 1000 and 1400 h each day, excluding the migration phase of the annual movement cycle. A second analysis assessed if, when weather changed from inversion conditions to standard lapse rates or vice versa, moose moved to higher or lower elevation to minimize their exposure to temperature variation.

Stable isotopes and diet

We assessed moose diets by comparing δ13C and δ15N signatures measured in moose guard hairs collected at summer captures with those measured in potential forages within Old Crow Flats, capitalizing on the distinct δ13C signatures of terrestrial and aquatic plants, and δ15N differentiation across terrestrial plants (Milligan et al. 2010). Submerged aquatic vegetation included Siberian water-milfoil (*Myriophyllum sibiricum*, milf), alpine pondweed (*Potamogeton alpinus*, pwda), white-stem pondweed (*P. praelongus*, pwdw), and Richardson's pondweed (*P. richardsonii*, pwdr). Emergent aquatic plants sampled included yellow pond-lily (*Nuphar polysepala*, lily), northern bur-reed (*Sparganium hyperboreum*, brrd), white (water) sedge (*Carex aquatilis*, sdge) and water horsetail (*Equisetum fluviatile*, hrtl). Terrestrial plants sampled included tea-leaf willow (*Salix pulchra*, wlt), feltleaf willow (*S. alaxensis*, wlf), unidentified willow species (*S. spp*., wls), alder (*Alnus viridis*, ald), and dwarf birch (*Betula glandulosa*, dbr).

Guard hairs were collected from 12 moose (7 bulls, 5 cows) during the 2007 summer capture. Metabolically inert tissues such as hair reflect the diet during the period of growth and retain this dietary signature in chronological sequence (Darimont and Reimchen 2002, Ayliffe et al. 2004). The base portion of the hair represents the most recent dietary assimilation and the tip at an earlier period (Darimont and Reimchen 2002). Given that moose have a single annual molt in April-May (Franzmann and Schwartz 1997) which precedes spring melt in our study area, and that hair grows incrementally through summer into autumn, the base portion should represent the summer diet and the tip the diet prior to spring melt (Darimont and Reimchen 2002). We cut the guard hairs into 3 sections (base, middle, and tip) and assumed the base was reflective of the summer diet and the tip the late winter diet (Milligan 2010). Although we did not know specifically where moose were prior to sampling, given the annual fidelity to winter and summer ranges, we assigned individuals to the summer and winter ranges they occupied post-collar deployment.

Guard hair samples were prepared for continuous-flow isotope ratio mass spectrometry analysis at the Water and Aquatic Sciences Research Program at University of Victoria using a Costech 4010 Elemental Analyser coupled to a Therm Delta V Mass Spectrometer. We incorporated diet-to-hair fractionation values for mammalian herbivores based on meta-analyses of captive animal experiments from the literature and estimates for moose (+3.0‰ for δ13C and +2.7‰ for δ15N; McCutchan et al. 2003, Sponheimer et al. 2003a, 2003b, Vanderklift and Ponsard 2003, Tischler 2004, Schwertl et al. 2005). This correction involved subtracting 3.0‰ for δ13C and 2.7‰ for δ15N to account for dietary fractionation.

We used isotopic mixing models (IsoSource; Phillips and Gregg 2003) to estimate the contribution of shrubs and macrophytes in the diets. Plans with similar isotopic signatures were grouped together to meet the criteria for distinct dietary sources isotopic modeling (Gannes et al. 1997, Phillips and Gregg 2003). The 4 categories of plants were 1) willow (bark and leaves; *Salix* spp.), 2) feltleaf willow/alder/birch (bark and leaves; *S. alaxensis*, *Betula glandulosa*, and *Alnus crispa*), 3) a composite of emergent aquatic plants that represented emergent and submergent plants with similar isotopic values (including *Carex sp.*, *C. utriculata*, *C. aquatilus*, *Comarum palustre*, *Equisetum fluviatile*, *Sparganium sp.*, and *S. hyperboreum*), and 4) submerged aquatic plants (*Myriophyllum sibiricum*, *Potamogetonzosterifolium*, *P. richardsonii*, *P. pusillus*, *P. alpinus*, *P. praelongus*). In our IsoSource models, we examined all possible combinations of the models using source increments of 1‰ and mass balance tolerance values of 0.1%, which incorporate uncertainty to the models with a magnitude similar to measurement error and source variability in isotopic values (Phillips and Gregg 2003).

RESULTS

Migration, home range, and habitat selection

Seventeen of 19 moose were classified as migratory (Fig. 2a) moving to the northwest (n = 8), west (n = 4), or southeast (n = 5) from Old Crow Flats, and wintering at high ($\bar{x}$ = 733, range = 588–902 m), intermediate ($\bar{x}$ = 436, range = 387–502 m), and low elevations ($\bar{x}$ = 347, range = 292–488 m), respectively (Fig. 1); the 2 non-migratory animals remained in or near the southeastern portion of Old Crow Flats throughout the year. In each winter range, the maximum elevation occupied by bulls averaged 70–125 m higher than that of cows. The timing and duration of the autumn migration was highly variable, with the first moose leaving Old Crow Flats on 4 August and the last on 30 November. A peak in movement occurred in mid-September during a 15-day window (2–17 September) when 9 of 17 moose were migrating (Fig. 2b). The timing of spring migration back to Old Crow Flats also varied, with the first moose returning on 14 May and the last on 14 July. In general, spring migration peaked during a 15-day window (9 and 24 May) when 6 animals were migrating (Fig. 2b). The duration of the autumn migration varied between 2 and 201 days ($\bar{x}$ = 45 d, n = 17), and in spring between 2 and 102 days ($\bar{x}$ = 39 d, n = 14) (Fig. 2b). There were no gender differences in migration start dates or durations in autumn ($F_{1,15}$ = 0.676, P = 0.424; $F_{1,15}$ = 2.245, P = 0.155), or spring end dates or durations in spring ($F_{1,10}$= 0.006, P = 0.937; $F_{1,10}$ = 0.621, P = 0.449).

Migration distance (measured as maximum straight-line displacement distance from a summer and winter ranging location) varied from 59 to 144 km (n = 15 moose with complete winter data), and was 27 km longer ($F_{1,13}$ = 5.861, P = 0.030) for bulls ($\bar{x}$ = 111 ± 25 km (SD), n = 9) than cows ($\bar{x}$ = 84 ± 13 km (SD), n = 6) (Fig. 2c). Migration distance based on straight-line displacement distance measured from the last summer ranging location to the first winter ranging location varied from 26 to 135 km among the same 15 animals, and averaged 33 km further for bulls (84 ± 26 km) than cows (51 ± 22 km). Migratory path lengths travelled by these moose (the sum of location to location distances from the last summer ranging location to the first winter ranging location) varied from 39 to 326 km, and averaged 81 km further for bulls (165 ± 96 km) than cows (84 ± 44 km). Daily migratory path lengths were typically < 10 km/d, but the fastest migrants (2 cows and 1 bull) traveled ~20 km/d. The relationship between migratory path length and linear displacement, indicative of the relative straightness of a migratory route, averaged 0.65 (range = 0.34–0.91) and was somewhat more variable in bulls (range = 0.34–0.91) than cows (range = 0.52–0.89). Annual path lengths (total distance traveled in 365 consecutive days; n = 12 moose [2 non-migratory] with location data > 1 year in duration) ranged between 501 and 1099 km (708 ± 183 km). The 2 non-migratory cows had ~ 25% shorter path lengths (522 and 568 km) than the migratory cows (710 ± 134 km).

Home range size differed by season ($F_{1,24}$ = 6.913, P = 0.015) but not by sex ($F_{1,24}$ = 0.001, P = 0.975), with the significant correlation between estimated home range and

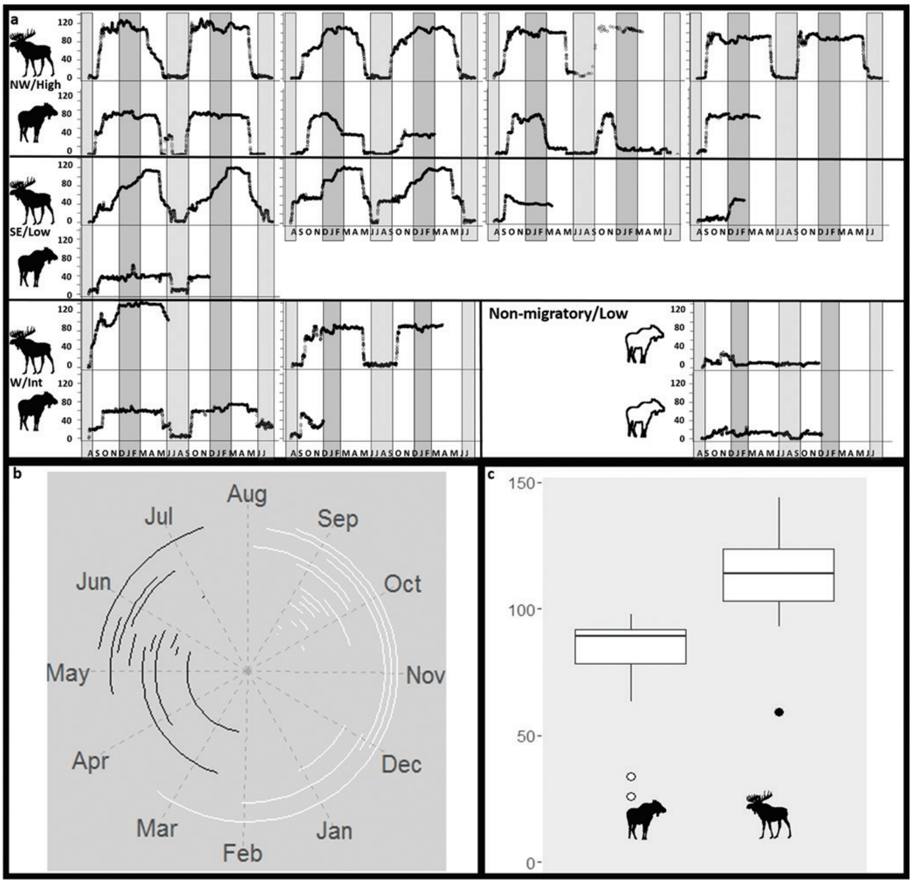

Fig. 2. Migratory pattern, distance, phenology, and sex differences for moose radio-collared in the study area. Panel (a) presents the displacement (km) between the first summer location and all subsequent relocations over time for 19 moose grouped by migration direction and elevation (northwest-high elevation, NW/High); west-intermediate elevation, W/Int); southeast-low elevation, SE/Low), by sex, and ordered by displacement within these categories. Two non-migratory cows are presented separately (outlined icons) and included in the SE/Low group. Light and dark gray shaded areas represent 3-month summer and winter seasons, respectively. Panel (b) is a circular plot showing the timing and duration of autumn (white lines, n = 17) and spring migration (black lines, n = 12) in the first year of the study; radial lines indicate the first day of each month. Panel (c) indicates sex differences in migration distance expressed as maximum displacement (km) for 9 bulls and 6 cows with complete winter data. The closed circle indicates 1 bull that migrated a shorter distance (59 km) than most, but was classified as migratory; the open circles are the 2 non-migratory cows.

the number of relocations ($F_{1,24}$ = 5.928, P = 0.022) accounted for as a covariate. Home range was smaller in summer (48 ± 33 km^2, range = 2–117 km^2) than winter (170 ± 164 km^2, range = 13–674 km^2) across the population and by individual (t_{paired} = −2.7885, df = 13, P = 0.0154). Based on significant coefficient estimates [log$_{10}$(HRS (km^2)) = 0.93177 + 0.0017666 * (number of locations) + 0.4799 * (0 summer, 1 winter)], the predicted home range size (200 relocations) in summer and winter was 19 and 58 km^2, respectively. Home range elevation was lower in summer (307 ± 10 m) than winter (648 ± 270 m) across the population ($F_{1,26} = 22.295$, $P < 0.001$) and by individual ($t_{\text{paired}} = -4.6651$, df = 13, $P < 0.001$).

Moose used resources differently in winter and summer at the second-order of habitat selection, and the "average" level of selection was strong (summer $XL2^2 - XL1^2 = 901,326$, 6 df, $P < 0.001$, winter $XL2^2 - XL1^2 = 110,303$, 6 df, $P < 0.001$). In summer, moose consistently used home ranges in drained lake basins and lake habitats, except for 1 animal in the southeast that used shrub and river habitat (Fig. 3, top left panel). In contrast, second-order selection in winter was individually and regionally variable (Fig. 3, top right panel). Moose at high elevation in the northwest established home ranges in barrens, river, shrub, and tundra habitats, whereas moose at intermediate (west) and low elevations (southeast) had home ranges in forested, shrub, or lake habitats, except 1 animal using drained lake basins.

At the third-order of habitat selection, habitat use in winter and summer was also selective and strong overall (summer $XL2^2 = 37,059$, 81 df, $P < 0.001$, winter $XL2^2 = 23,898$, 57 df, $P < 0.001$). In summer,

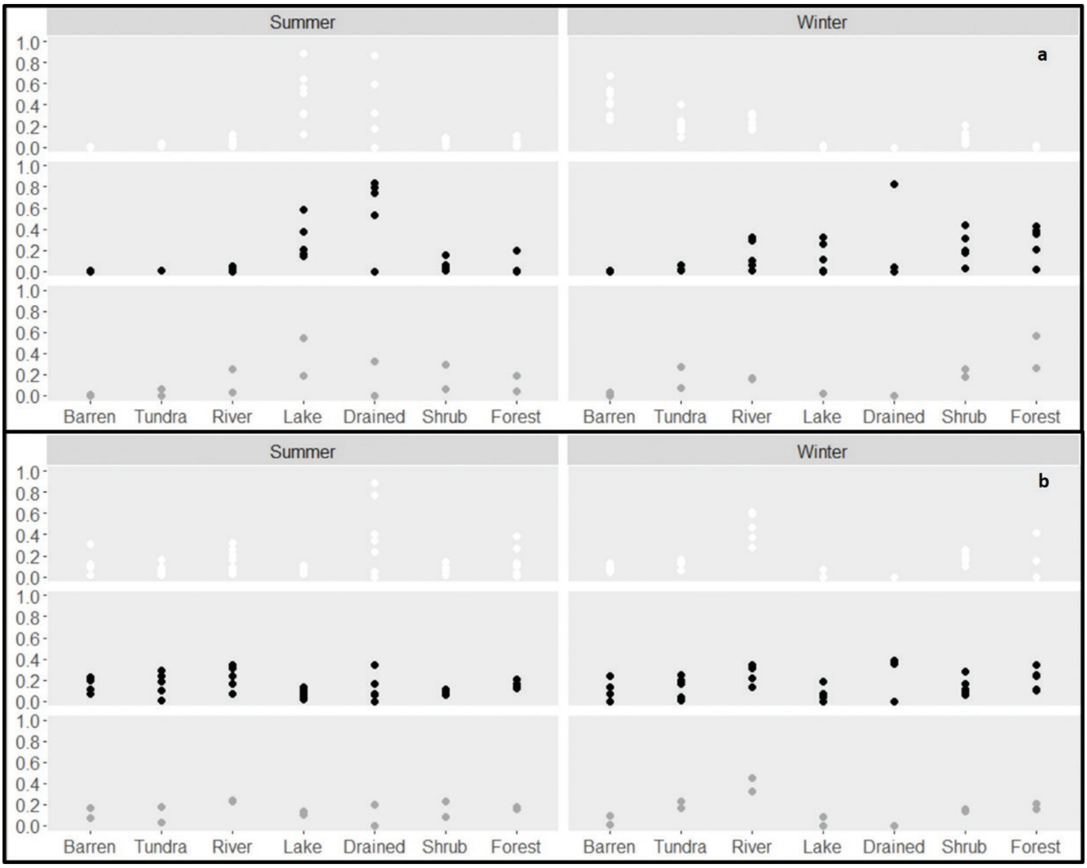

Fig. 3. Selection ratios for 7 habitat categories in summer (left) and winter (right) at a) the second order scale (home range) and b) the third order scale (locations within home range). Colors indicate selection ratios for moose wintering in the northwest at high elevation (white, n = 7), in the southeast at low elevation (black, n = 5 including the 2 non-migratory cows), and in the west at intermediate elevation (grey, n = 2).

third-order habitat selection was inconsistent among moose, with some most likely to use locations in drained lake basins, and others in river habitats or forested, barren, or tundra habitat (Fig. 3, bottom left panel). In contrast, third-order habitat use was individually and regionally consistent in winter. Most selected strongly for river habitats, particularly those at high elevation in the northwest. The few outliers included single animals in forested habitat at high (northwest) and intermediate elevation (southeast), and 2 animals in drained lake basins at low elevation in the southeast (Fig. 3, bottom right panel).

Drained lake basins were used preferentially during summer at all selection scales. At the broadest level, moose concentrated summer activity in Old Crow Flats where drained lake basins are a major landscape feature. At the second order of selection, drained lake basins averaged 6% (0–25%, n = 14) of home ranges but only 0.2% of available habitat in the entire study area and 3% of Old Crow Flats (Table S1). Conversely, drained lake basins were not strongly or consistently selected for at the third order of selection across the population (Fig. 3). However, 26–46% of summer locations for 5 animals were in drained lake basins, 2–40 × higher than expected based on availability in their home ranges.

Influence of air temperature

In 2008, $T_{a\text{-}OC}$ ranged between a maximum of 27°C on 23 June 2008 at 1800 h and a minimum of −49°C on 31 January 2008 at 1100 hr. Similarly, between 1100 and 1300 h on 31 January, T_c averaged −42°C (range = −40 to −43°C) for 7 moose located at < 500 m elevation; T_c was much warmer (range = −26 to −27°C, Fig. 4a) for 2 moose at > 800 m elevation. This inversion of increasing temperature with increasing elevation ($R^2 = 0.8$, $P < 0.001$) was not constant over time. For example, by 24 February 2008, T_c at high elevation (600–800 m) was cooler (ave. = −23, range = −22 to −25°C) than at low elevation (<350 m) (ave. = −16, range = −18 to −13°C; $R^2 = 0.6$, $P = 0.001$, Fig. 4a). Fitting a GAM to T_c identified a significant interaction of date and elevation, consistent with strong winter inversions when T_a in December-January-February averaged 9°C warmer at 1250 m than at 250 m, and standard lapse rates in autumn when T_a in September-October was approximately 6°C cooler at 1250 m than 250 m. However, the patterns of variation in T_c at different elevations suggested that even in mid-winter, conditions frequently alternated between strong and weak inversions, and standard lapse rates (Fig. 4b). Comparing $T_{a\text{-}OC}$ to T_c for 3 moose that remained at low elevation throughout the study period indicated that T_c closely tracked variation in $T_{a\text{-}OC}$ with additional influence of season (consistent with changes in pelage insulation), day-night (consistent with solar radiation), land cover (consistent with thermal cover), and T_a (controlling for all other variables; Fig. S3).

Winter occupation of high elevations permitted moose to marginally reduce their exposure to cold extremes, while their consistent summer use of low elevations resulted in exposure to warm extremes. When available temperatures (T_{a,e_x,t_y}) were between −30 and −40°C, it was 3.5°C warmer, on average, for the highest than lowest elevation moose (Fig. 5). Extremely cold temperatures ($T_c < -40$°C; n = 1646 records) were rarely measured for moose at elevations > 800 m (8% of 1646 records), but were more frequent at < 600 m (62% of 1646 records). Two-phase regression analysis of T_c (across the range of occupied elevations) and $T_{a\text{-}OC}$ indicated that for 7 high elevation moose, T_c began to decouple from $T_{a\text{-}OC}$ at an average $T_{a\text{-}OC}$ threshold of −13.8°C (range = −22.5 to

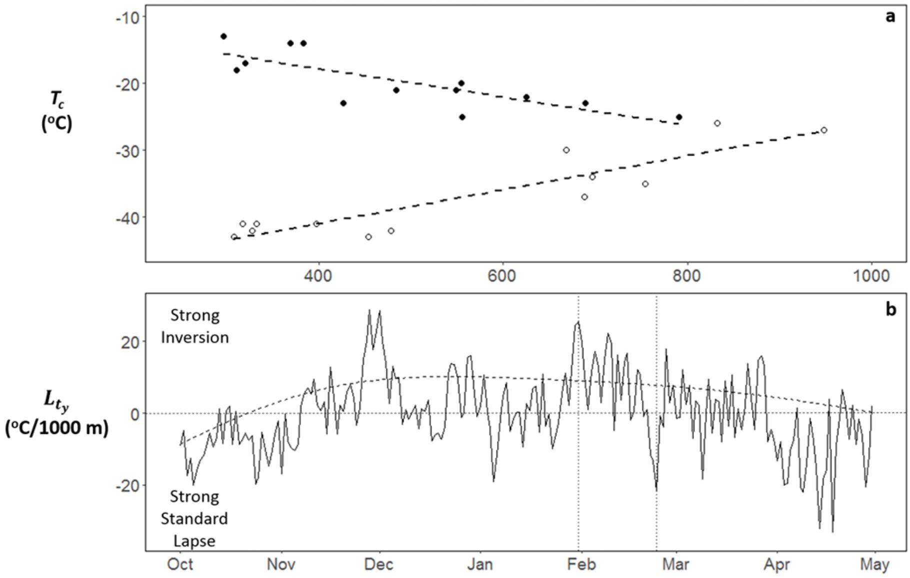

Fig. 4. Elevation-related variation in winter air temperatures in and around Old Crow Flats, Yukon as measured by radio-collars (T_c; n = 13). Panel (a) presents the relationship between T_c and elevation (m) between 1200 and 1600 h on 31 January 2008, the coldest day of winter 2007–2008 which was characterized by a strong thermal inversion (open circles); the same relationship is presented between 800 and 1200 h on 24 February, a warmer day characterized by a strong standard lapse rate (closed circles). Panel (b) presents seasonal prevalence and finer scale temporal variation in this relationship from 1 October 2007 to 30 April 2008. The vertical axis indicates the lapse rate (L_{t_y} ; change in T_c /1000 m in elevation) with positive values indicating thermal inversions and negative values indicating standard lapses. The solid line indicates the daily linear relationship between 1000 and 1400 hr. The dashed line indicates values predicted for 1200 h in tundra habitat by a GAM model including time of day, day interacting with elevation, and habitat category. The first and second vertical dotted lines indicate the 2 days presented in panel (a).

−3.2°C); below this threshold, for every 10°C decline in $T_{a\text{-}OC}$, T_c declined on average 5.8°C (range = 4.9 to 6.6°C). In contrast, for 7 low and intermediate elevation moose, the decoupling of T_c and $T_{a\text{-}OC}$ occurred at a lower threshold (average = −23.3°C, range = −46.8 to −5.4°C) and was stronger; for every 10°C decline in low elevation $T_{a\text{-}OC}$ below the 2-phase threshold, T_c declined on average 10.7°C (range = 6.2 to 32.4°C) (Fig. S4). Nevertheless, the magnitude of cold avoidance was small relative to the range of temperatures moose were potentially exposed to across the 225–1250 m elevation profile within the annual range of the study population (Fig. S4). The T_c was consistently intermediate within this range, including during cold extremes and among moose at all elevations (Fig. S4). The only exception was when T_c was consistently close to the maximum available during the warmest summer temperatures, because nearly all moose were located at low elevations where temperatures were warmest.

Finally, the mid-day movement distance of moose (restricted to ranging phases of the annual movement cycle) did not vary consistently with T_c (Fig. S5) at any elevation. In winter, when conditions reversed from strong inversions to strong standard lapse

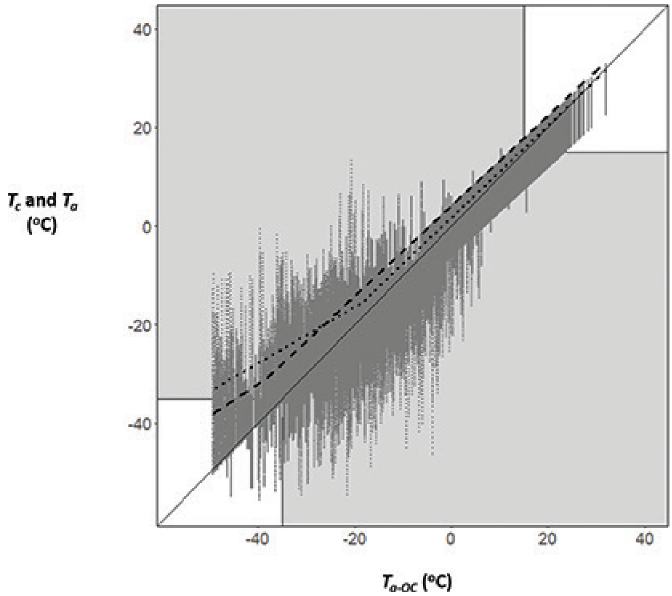

Fig. 5. The relationship between T_c (used) and T_a (available) throughout the study area and study period; these measurements are presented for every 4-h block from 3 August 2007 to 5 August 2009 (situated on the x-axis) according to ambient temperature ($T_{a\text{-}OC}$) recorded at Old Crow airport (251 m elevation) during the same 4-h block. Available temperatures (grey circles) were estimated for each 4-h block across 25 m increments from 225 to 1250 m (see Methods and Table S2). Black lines indicate used temperatures based on the relationship between T_c and $T_{a\text{-}OC}$ using a 2-phase linear regression. The relationships for 2 moose are presented; one occupied the highest annual average elevation (dotted black line) and one the lowest annual average elevation (dashed black line) relative to all moose (see Fig. S4). The black solid line is the 1-to-1 line. The corner boxes indicate temperatures below the estimated lower and upper critical temperatures of moose in winter (<−35°C) and summer (>15°C), respectively (Renecker and Hudson 1986).

rates or from standard lapse to inversion conditions, moose did not move in elevation to minimize T_c variation or avoid temperature extremes (Fig. S6).

Stable isotope and diet

Summer and late winter diets of moose, as inferred by stable isotope signatures of hair samples relative to vegetation, were consistent with an annual shrub-dominated diet, especially willow, dwarf birch, and/or alder (*Alnus crispa*) (Fig. 6). Submerged aquatic vegetation had enriched δ13C relative to terrestrial vegetation, with emergent aquatic vegetation intermediate of the two. Terrestrial vegetation differed primarily in δ15N enrichment, with all aquatic vegetation characterized by similar δ15N signatures intermediate of the least and most enriched terrestrial vegetation. In general, moose had low enrichment of δ13C and δ15N, with mixing models indicating a diet dominated by terrestrial shrubs (ca. 60% including various willow species, dwarf birch, and/or alder), followed in importance by emergent vegetation (ca. 25% mostly water sedge and horsetail) and submerged vegetation (<15% including *Potamogeton* and *Myriophyllum*).

In summer, δ13C signatures in moose were consistent with the importance of terrestrial versus aquatic vegetation, whereas in late winter, most variation was in δ15N

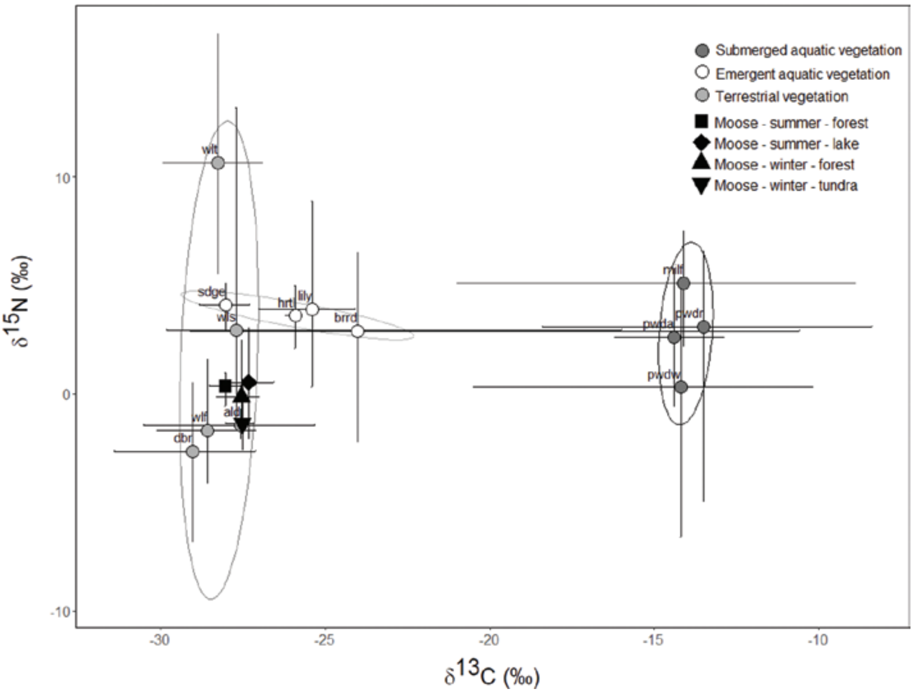

Fig. 6. The δ13C and δ15N signatures measured in moose hair and vegetation collected in the study. The hair signatures are adjusted by a fractionation constant (see Methods). Vegetation signatures are for plants collected in and around Old Crow Flats as measured by Milligan (2010) and include 4–6 species of submerged aquatic plants (dark grey), 4 species of emergent aquatic plants (white), and 5 species of terrestrial plants (light grey) (species codes in Methods). Ellipses show standard deviations (75% CI) for the mean isotopic values of the three vegetation categories.

signatures consistent with the importance of terrestrial species. In summer specifically, moose in lake-dominated home ranges had slightly higher δ13C signatures indicating higher use of aquatic vegetation compared to moose in forest-dominated home ranges with δ13C signatures indicating higher use of terrestrial shrubs ($F_{1,10} = 5.381$, $P < 0.05$) (Fig. 6). In late winter when aquatic plants are unavailable, moose occupying home ranges predominated by alpine habitat had δ15N signatures indicating higher use of feltleaf willow, dwarf birch, and/or alder than moose with home ranges in forest-dominated habitat which had δ15N signatures indicating higher use of tealeaf willow ($F_{1,10} = 2.083$, $P = 0.18$) (Fig. 6). Bulls and cows spending late winter in forest-dominated home ranges or summering in lake-dominated home ranges had similar δ13C and δ15N signatures.

DISCUSSION

The Old Crow Flats moose population is characterized by seasonal movement patterns and habitat selection, reflective of the extreme seasonality of the subarctic-to-arctic landscape where this population lives. The landscape transitions from a highly productive, food-rich wetland in summer to a winter landscape dominated by lake ice (shallow lakes comprise 40% of the surface area), snow, and cold air drainage. Accordingly, moose concentrate activity in Old Crow

Flats during summer, arriving there around spring thaw and leaving in late summer for autumn and winter ranges in alpine valleys widely dispersed around Old Crow Flats. Old Crow Flats is already a large landscape covering > 5,600 km^2, and moose migration into the surrounding mountains extends the ecological reach of Old Crow Flats to an area 14 × larger based on spatial locations (100% minimum convex polygon) of the 19 study moose captured and radio-collared in Old Crow Flats. This behavior renders Old Crow Flats a central foraging place (sensu (Boyd et al. 2014)) that moose return to year after year from multiple distant wintering sites.

The annual movement patterns indicate that moose summering in Old Crow Flats are mostly migratory, with ~ 90% migrating 50–150 km between summer and winter ranges. The average and maximum migration distances (bulls = 111 and 144 km; cows = 84 and 98 km) were somewhat shorter than those for the same study population captured and radio-collared on their winter range and estimated with the same method (average = 123 km, maximum = 196 km; Mauer 1998). Most moose displayed inter-annual consistency in migration timing, fidelity to winter and summer ranges, and migratory routes between these ranges. Migration tracks were relatively straight (average linear displacement/path length = 0.65) given the topographical complexity of the landscape, possibly reflecting limited effects of terrain and land cover on migratory paths and travel rate and warranting further quantitative assessment. Both our and Mauer's (1998) studies confirm that the summer population of moose in Old Crow Flats lies at the extreme of moose migratory behaviour in North America (LeResche 1974, Van Ballenberghe 1977, Demarchi 2003, White et al. 2014). Migration from the North Atlantic coast in Norway to Sweden's inland boreal forests is another example of long distance movement (31–171 km), yet opposite in that moose move from high elevations in summer to low coastal elevations in winter (Bunnefeld et al. 2011).

Moose returned to Old Crow Flats coincident with spring breakup, but many leave Old Crow Flats well before the onset of autumn freeze up and prior to the September and early October breeding season (Mauer 1998). Although bulls migrated farther than cows, the timing of movement (onset, halfway, and completion) was similar for both sexes. It is possible that a nutritional decline in forage quality occurs late in the growing season in Old Crow Flats, and moose seek higher quality forage at higher elevations where spring green-up and autumn senescence occur later, and moose density and herbivory are low in summer.

In summer, moose situate their home ranges where more lakes and drained lakes are available in Old Crow Flats than at higher elevations. The isotope composition of moose hair collected in Old Crow Flats was consistent with a year-round, shrub-dominated diet supplemented with aquatic vegetation in summer, particularly for moose using substantial lake habitat. Analysis of fecal samples from the study moose yielded similar results (Milligan 2010). These data indicate that moose in Old Crow Flats use and select drained lake basins, but also that use and selection varies individually and seasonally. A previous resource selection function analysis of these data indicated that, within the home range scale, moose in Old Crow Flats are more likely to use areas closer to water with a higher proportion of upright shrubs, higher diversity of vegetation types in the vicinity, and drained lake basins if present (Clarke et al. 2017). Home range size was much smaller in summer than winter, suggesting that availability of high quality forage in summer reduces space use more so than deep snow in winter (Phillips et al. 1973, Timmermann and McNicol 1988, van Beest et al. 2011). Overall, the shrub-dominated diet supplemented by aquatic vegetation in summer conforms with the typical year-round diet of most moose populations (Timmermann and McNicol 1988).

The moose population that summers in Old Crow Flats breaks into 3 largely distinct subpopulations during winter. One subpopulation summers on the west and north sides of Old Crow Flats and migrates mainly northwest to higher elevations (600–900 m), where they join moose from the Upper Coleen drainage in Alaska, the Firth River drainage in Canada and Alaska, and as far as the Kongakut River in Alaska (Mauer 1998). A second subpopulation summers on the west and south sides of Old Crow Flats and migrates mainly west to moderately higher elevations (400–500 m) within the lower drainages of the Coleen River in Alaska. The migration of these 2 subpopulations was described by Mauer (1998) who noted that the westward migrating subpopulation occasionally reaches the upper reaches of the Sheenjek River drainage 50 km west of the Coleen River drainage. A third subpopulation using the eastern portion of Old Crow Flats in summer either remains resident year-round locally in Little Flat where forested habitat comprises 26% of land cover compared to 12% elsewhere in Old Crow Flats, or migrates southeasterly towards low elevation winter ranges along the Porcupine, Driftwood, and Bell Rivers. If non-migratory moose are considered a distinct subpopulation, then the summer population in Old Crow Flats consists of 4 subpopulations – 3 migratory and 1 resident.

Moose at high elevations in winter, especially the northwest subpopulation, selected for shrub cover close to rivers and streams within long and narrow home ranges situated at the bottom of alpine valleys. Moose at low elevations in winter, especially the southeast subpopulation, occupied variably shaped home ranges that tended to be close to streams or rivers and composed of more forested and shrub habitat than surrounding areas. Stable isotope analysis indicated that moose in alpine riparian habitats had δ15N signatures indicative of greater use of low enrichment shrubs like feltleaf willow and dwarf birch than moose occupying home ranges predominated by forest habitat with δ15N signatures indicating higher use of tealeaf willow. These results are consistent with previous research with Alaska-Yukon moose indicating greater use and preference of higher-growing, more nutritious feltleaf willow than lower-growing, less nutritious tealeaf willow, except in forested habitats where tealeaf willow can be the only abundant shrub (Risenhoover 1989).

Our findings are consistent with Mauer's (1998) speculation that seasonal migration from Old Crow Flats to surrounding higher elevations allows moose to avoid the coldest winter temperatures at low elevations where average snowpack may also be deeper and winds more substantial. We lack the data on elevation- and land cover-specific snow accumulations across the study area to directly evaluate the possibility of snow avoidance. The frequency and magnitude of inversions detected from T_c aligned well with patterns detected by meteorological studies using weather balloons (Bourne et al. 2010). On most days, the T_c for moose at 1000 m was 5–15°C warmer than that for moose at 350 m. The lower critical temperature of moose in Alberta is estimated as about −35°C (Renecker and Hudson 1986), and large body size and cold acclimatization likely provides increased thermoregulatory ability for this Alaska-Yukon subspecies. We found no evidence that moose moved more on the coldest days or responded to the dynamic nature of inversions by moving up when temperatures were warmer at high elevations or down when warmer at lower elevation. Furthermore, several moose remained at low elevation throughout winter, exposing themselves to the consistently colder conditions there. Even in the extreme winter climate that prevails in this subarctic environment, thermoregulation is likely a minor cost of the daily energy budget of moose in all but the coldest conditions.

Although we focus here on snow and temperature as an explanation for seasonal moose migration, spatial variation in predation risk may be an additional factor influencing migration and habitat selection in this region. For example, the risk of predation by wolves and bears may be minimal in Old Crow Flats during the open water season, whereas the risk of wolf predation in winter may be lessened by occupying isolated alpine valleys. Speculation regarding season- and habitat-specific predation risk warrants further examination.

Vuntut Gwitchin knowledge of moose in Old Crow Flats predicted our habitat selection and dietary results, including interannual home range fidelity in summer, habitat preference for locations in and around drained lake basins and close to other water bodies, and dietary reliance on shrubs. Other research in Old Crow Flats also confirms local observations regarding recent climate warming (Porter and Pisaric 2011), increased frequency of lake drainages in this landscape (Lantz and Turner 2015), shrub growth trajectories associated with these drainages (Lantz 2017), and permafrost degradation particularly along exposed shorelines (Turner et al. 2014, Roy-Léveillée and Burn 2016). While an assessment of climate change impacts on moose habitat in Old Crow Flats was beyond the scope of this study, our results suggest that moose benefit from proliferation of shrubs in drained lake basins that are a major contemporary feature of the Old Crow Flats. Further, our results reinforce the concept that the continuity of a habitat mosaic within Old Crow Flats is important in providing moose spatial proximity to water and access to a diversity of vegetation, including seasonally high use of aquatic vegetation.

From a habitat protection and conservation perspective, the core habitat and winter ranges of the 3 subpopulations of the Old Crow Flats moose population is well protected. The Old Crow Flats wetland complex is protected under Vuntut Gwitchin First Nation Final Agreement Category A Lands, Vuntut National Park, and the Old Crow Flats Special Management Plan, with lands

> "to be protected and managed in a manner that permanently protects the ecological integrity of the Flats, including its diversity, its fish and wildlife populations and its habitats from activities that could reduce the land's capability, while maintaining access to this area by Vuntut Gwitchin citizens for traditional and current harvesting of fish and wildlife resources." (TWGMC 2006: 38).

The entirety of the migratory routes and winter ranges of the northwest and west subpopulations is protected in Canada by Vuntut National Park and Ivvavik National Park and in Alaska by the Arctic National Wildlife Refuge. Although the migratory routes and winter range of the southeast population are largely outside of Category A lands or the Old Crow Flats Special Management Unit (except for the Driftwood River), they are designated as low development zones within the North Yukon Regional Land Use Plan, indicative of locations with

> "High ecological and heritage/cultural values" where "Maintaining ecological integrity, protecting heritage and cultural resources, and minimizing land use impacts is the priority." (North Yukon Planning Commission 2009).

In terms of moose harvest, Vuntut Gwitchin have subsistence harvest rights across nearly all of this population's Canadian distribution including Vuntut National Park and (contingent on the Inuvialuit harvester agreement) Ivvavik National Park. The southeastern subpopulation is subject to licensed harvest in the Yukon, and subsistence and recreational harvest is permitted within the Arctic National Wildlife Refuge in Alaska. However, given the remoteness and seasonal movement patterns of this population, hunting pressure and harvest are limited. Summer and autumn boat travel to Old Crow Flats is often prevented by low water levels in the Old Crow River, and by the time hunters can reach Old Crow Flats by snow and ice, most moose have migrated to winter ranges where they remain until travel by snow and ice is impossible; hunters do have winter access to moose that remain resident in the southeast. Furthermore, the winter ranges of the northwestern and western subpopulations are largely outside of Canada, and too distant and mountainous for easy access from the community of Old Crow. However, the southeast subpopulation is likely accessible to boat-based hunters in autumn especially along the Porcupine River, and in winter throughout much of its winter range. Any recreational and subsistence moose harvet occurring in the eastern side of the Arctic National Wildlife Refuge, whether in autumn or winter, likely includes moose summering in Old Crow Flats. Accordingly, monitoring population and harvest trends in Yukon, particularly around the Porcupine River and the southeastern portion of Old Crow Flats, and in Alaska within the Arctic National Wildlife Refuge, is important for the conservation status and management of this population.

The YNNK Old Crow IPY project offers a model of community leadership in research, including how Indigenous knowledge and scientific research can be combined to identify knowledge needs, then broaden ecological knowledge of locally important landscapes and wildlife populations (Wolfe et al. 2011, Brunet et al. 2014). The Gwitchin project title, Yeendoo Nanh Nakhweenjit K'atr'ahanahtyaa translates, roughly, as "taking care of the land for the future." The local knowledge and research described here reveals the enormity of the land base supporting a single moose population, how extreme seasonality in climate manifests as extreme seasonality in behaviour and habitat use, and the resulting complexity of climate change impacts on moose and moose habitat at the periphery of the species range. The uniqueness of the landscape of Old Crow Flats and surrounding uplands, the migratory moose population that resides there, the Vuntut Gwitchin's reliance on this landscape and its wildlife resources, and the magnitude of locally observed and anticipated climate change impacts combine to motivate continued international monitoring and conservation of these vital landscapes, natural resources, and human-nature relationships in a collaborative "taking care of the land for the future."

ACKNOWLEDGEMENTS

We thank the people of Old Crow, especially the elders and hunters, for allowing us to learn together about their lands and wildlife, for hosting us in their community, for their permission to deploy collars on moose, and for keeping us safe on their lands. W. Josie, D. Matthiesson, S. Foss, B. Bell, and M. Williams provided critical assistance and insight in framing the initial collaboration and guiding it from the idea stage through fieldwork. R. Ward provided useful insights into moose ecology, helped with the project design, and generously loaned us collars on short notice. M. Oakley and M. Kienzler ably assisted with moose captures, collar deployments, and recoveries. The many researchers and graduate students involved in other components of the Old Crow IPY project were critical to the success of the overall project and helped us to situate moose ecology within the physical and biological landscape of Old Crow Flats. Finally, referees and editors provided helpful comments on the manuscript.

REFERENCES

Allenby, R. J. 1989. Clustered, rectangular lakes of the Canadian Old Crow Basin. Tectonophysics 170: 43–56. doi:10.1016/0040-1951(89)90102-9

Ayliffe, L., T. E. Cerling, T. Robinson, A. Wes, M. Sponheimer, B. Passey, J. Hammer, B. Roeder, M. -D. Dearing, and J. R. Ehleringer. 2004. Turnover of carbon isotopes in tail hair and breath CO^2 of horses fed an isotopically varied diet. Oecologia 139: 11–22. doi:10.1007/s00442-003-1479-x

Balasubramaniam, A. M., R. I. Hall, B. B. Wolfe, J. N. Sweetman, and X. Wang. 2015. Source water inputs and catchment characteristics regulate limnological conditions of shallow subarctic lakes (Old Crow Flats, Yukon, Canada). Canadian Journal of Fisheries and Aquatic Sciences 72: 1058–1072. doi:10.1139/cjfas-2014-0340

Ball, J. P., G. Ericsson, and K. Wallin. 1999. Climate changes, moose and their human predators. Ecological Bulletins 47: 178–187.

_____, C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose Alces alces ranges in northern Sweden. Wildlife Biology 7: 39–48. doi:10.2981/wlb.2001.007

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. doi:10.1007/s00442-011-2072-3

Bourne, S. M., U. S. Bhatt, J. Zhang, and R. Thoman. 2010. Surface-based temperature inversions in Alaska from a climate perspective. Atmospheric Research 95: 353–366. doi:10.1016/j.atmosres.2009.09.013

Boyd, C., A. Punt, H. Weimerskirch, and S. Bertrand. 2014. Movement models provide insights into variation in the foraging effort of central place foragers. Ecological Modelling 286: 13–25. doi:10.1016/j.ecolmodel.2014.03.015

Bradley, R. S., F. T. Keimig, and H. F. Diaz. 1992. Climatology of surface-based inversions in the North American Arctic. Journal of Geophysical Research: Atmospheres 97: 15699–15712. doi:10.1029/92JD01451

Brunet, N., G. Hickey, and M. M. Humphries. 2014. Understanding community-researcher partnerships in the natural sciences: a case study from the Arctic. Journal of Rural Studies 36: 247–261. doi:10.1016/j.jrurstud.2014.09.001

Bunnefeld, N., L. Borger, B. Van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80: 466–476. doi:10.1111/j.1365-2656.2010.01776.x

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516–519. doi:10.1016/j.ecolmodel.2006.03.017

Clarke, H., D. Cooley, M. M. Humphries, M. Landry-Cuerrier, and T. Lantz. 2017. Summer habitat selection by moose on the Old Crow Flats. Yukon Fish and Wildlife Branch Report MR-17-01. Whitehorse, Yukon, Canada.

Darimont, C. T., and T. E. Reimchen. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. Canadian Journal of Zoology 80: 1638–1642. doi:10.1139/z02-149

DeCesare, N. J., J. R. Newby, and J. M. Ramsey. 2015. A review of parasites and disease impacting moose in North America. Intermountain Journal of Sciences 21: 62.

Demarchi, M. W. 2003. Migratory movements and home range size of moose in the central Nass Valley, British Columbia. Northwestern Naturalist 84: 135–141. doi:10.2307/3536539

Franzmann, A. W., and C. C. Schwartz. 1997. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, DC, USA.

Gannes, L. Z., D. M. O'Brien, and C. Martinez del Rio. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology 78: 1271–1276. doi:10.1890/0012-9658(1997)078[1271:SIIAEA]2.0.CO;2

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84: 1–50.

Goddard, J. 1970. Movements of moose in a heavily hunted area of Ontario. The Journal of Wildlife Management 34: 439–445. doi:10.2307/3799030

Hauge, T. M., and L. B. Keith. 1981. Dynamics of moose populations in northeastern Alberta. The Journal of Wildlife Management 45: 573–597. doi:10.2307/3808692

Hayes, R., and N. Barichello. 1986. Wolf, moose, muskoxen and grizzly bear observations on the Yukon North Slope. Yukon Department of Environment, Whitehorse, Yukon, Canada.

Houston, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming. Technical Bulletin Number 1. Grand Teton Natural History Association, Moose, Wyoming, USA.

Jenkins, K. J., and R. G. Wright. 1987. Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. Canadian Journal of Zoology 65: 1397–1401. doi:10.1139/z87-220

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71. doi:10.2307/1937156

Jones, H., P. J. Pekins, L. E. Kantar, D. Ellingwood, I. Sidor, A. Lichtenwalner, and M. O'Neil. 2019. Mortality assessment of calf moose during successive years of winter tick epizootics in New Hampshire and Maine. Canadian Journal of Zoology 97: 22–30. doi:10.1139/cjz-2018-0140

Jung, T. S., T. E. Chubbs, C. G. Jones, F. R. Phillips, and R. D. Otto. 2009. Winter habitat associations of a low-density moose (*Alces americanus*) population in central Labrador. Northeastern Naturalist 16: 471–480. doi:10.1656/045.016.n313

Lantz, T. C. 2017. Vegetation succession and environmental conditions following catastrophic lake drainage in Old Crow Flats, Yukon. Arctic 70: 177–189. doi:10.14430/arctic4646

_____, and K. Turner. 2015. Changes in lake area in response to thermokarst processes and climate in Old Crow Flats, Yukon. Journal of Geophysical Research: Biogeosciences 120: 513–524. doi:10.1002/2014JG002744

Lauriol, B., D. Lacele, S. Labreque, C. R. Duguay, and A. Telka. 2009. Holocene evolution of lakes in the Bluefish Basin, Northern Yukon, Canada. Arctic 6: 212–224. doi:10.14430/arctic133

Lenarz, M. S., M. E. Nelson, M. W. Schrage, and A. J. Edwards. 2009. Temperature mediated moose survival in northeastern Minnesota. The Journal of Wildlife Management 73: 503–510. doi:10.2193/2008-265

LeResche, R. 1974. Moose migrations in North America. Naturaliste Canadien 101: 393–415.

LOISA, K., and E. PULLIAINEN. 1968. Winter food and movements of two moose (*Alces alces* L.) in northeastern Finland. Annales Zoologici Fennici 5: 220–223.

MANLY, B., L. MCDONALD, D. L. THOMAS, T. L. MCDONALD, and W. P. ERICKSON. 2007. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media, New York, New York, USA.

MAUER, F. 1998. Moose migration: northeastern Alaska to northwestern Yukon territory, Canada. Alces 34: 75–81.

MCCUTCHAN, J. H., W. M. LEWIS, C. KENDALL, and C. C. MCGRATH. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378–390. doi:10.1034/j.1600-0706.2003.12098.x

MILLIGAN, H. E. 2010. Seasonal and spatial variability of aquatic and terrestrial feeding by moose in Old Crow Flats, Yukon. Special Report. Environment Yukon, Whitehorse, Yukon, Canada.

MILLIGAN, H. E., T. D. PRETZLAW, and M. M. HUMPHRIES. 2010. Stable isotope differentiation of freshwater and terrestrial vascular plants in two subarctic regions. Ecoscience 17: 265–275. doi:10.2980/17-3-3282

MONTEITH, K. L., R. W. KLAVER, K. R. HERSEY, A. A. HOLLAND, T. P. THOMAS, and M. J. KAUFFMAN. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. Oecologia 178: 1137–1148. doi:10.1007/s00442-015-3296-4

MOSSOP, D. H. 1975. Moose Counts – Old Crow 1974 and 1975. Environment Yukon, Whitehorse, Yukon, Canada.

_____. 2015. The changing ecology of the Old Crow Flats. Yukon Research Centre, Yukon College, Whitehorse, Yukon, Canada.

MUGGEO, V. M. R. 2017. Regression models with break-points / change-points estimation. R Package Version 37.

NATION, V. G. F., and S. SMITH. 2010. People of the lakes: stories of our Van Tat Gwich'in Elders/Googwandak Nakhwach'anjoo Van Tat Gwich'in. University of Alberta, Edmonton, Alberta, Canada.

NORTH YUKON PLANNING COMMISSION. 2009. North Yukon Regional Land Use Plan. Whitehorse, Yukon, Canada. http://www.emr.gov.yk.ca/rlup/north-yukon-regional-land-use-plan.html (accessed September 2019).

OVENDEN, L. 1986. Vegetation colonizing the bed of a recently drained thermokarst lake (Illisarvik), Northwest Territories. Canadian Journal of Botany 64: 2688–2692. doi:10.1139/b86-354

PHILLIPS, D. L., and J. W. GREGG. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261–269. doi:10.1007/s00442-003-1218-3

PHILLIPS, R. L., W. E. BERG, and D. B. SINIFF. 1973. Moose movement patterns and range use in northwestern Minnesota. The Journal of Wildlife Management 37: 266–278. doi:10.2307/3800117

PORTER, T. J., and M. F. PISARIC. 2011. Temperature-growth divergence in white spruce forests of Old Crow Flats, Yukon Territory, and adjacent regions of northwestern North America. Global Change Biology 17: 3418–3430. doi:10.1111/j.1365-2486.2011.02507.x

PULLIAINEN, E. 1974. Seasonal movements of moose in Europe. Le Naturaliste Canadien 101: 379–392.

QGIS DEVELOPMENT TEAM. 2016. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org (accessed September 2019).

R CORE TEAM. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (accessed September 2019).

Ramsar Convention. 2004. The List of Wetlands of International Importance. Ramsar Secretariat, Gland, Switzerland.

Renecker, L. A., and R. J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology 64: 322–327. doi:10.1139/z86-052

_____, and C. C. Schwartz. 1998. Nutrition and energetics. Pages 403–440 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution, Washington, DC, USA.

Risenhoover, K. L. 1989. Composition and quality of moose winter diets in interior Alaska. The Journal of Wildlife Management 53: 568–577. doi:10.2307/3809178

Rolandsen, C. M., E. J. Solberg, B. E. Saether, B. V. Moorter, I. Herfindal, and K. Bjorneraas. 2017. On fitness and partial migration in a large herbivore–migratory moose have higher reproductive performance than residents. Oikos 126: 547–555. doi:10.1111/oik.02996

Roy-Léveillée, P., and C. Burn. 2010. Permafrost conditions near shorelines of oriented lakes in Old Crow Flats, Yukon Territory. Pages 1509–1516 *in* Conference Proceedings of GEO, 12–16 September, 2010 Calgary, Alberta, Canada.

_____, and _____. 2016. A modified landform development model for the topography of drained thermokarst lake basins in fine-grained sediments. Earth Surfaces Processes and Landforms 41: 1504–1520. doi:10.1002/esp.3918

_____, _____, and I. D. McDonald. 2014. Vegetation-permafrost relations within the treeline ecotone near Old Crow, northern Yukon, Canada. Permafrost and Periglacial Processes 25: 127–135. doi:10.1002/ppp.1805

Russell, D., D. Mossop, and C. Goodfellow. 1978. Remote sensing for waterfowl nesting and nesting habitat in Old Crow Flats, Yukon Territory, Canada. PECORA IV–Conference, Sioux Falls, South Dakota, USA.

Schuster, R. C., E. E. Wein, C. Dickson, and H. M. Chan. 2011. Importance of traditional foods for the food security of two First Nations communities in the Yukon, Canada. International Journal of Circumpolar Health 70: 286–300. doi:10.3402/ijch.v70i3.17833

Schwertl, M., K. Auerswald, R. Schaufele, and H. Schnyder. 2005. Carbon and nitrogen stable isotope composition of cattle hair: ecological fingerprints of production systems? Agriculture, Ecosystems & Environment 109: 153–165. doi:10.1016/j.agee.2005.01.015

Singh, N. J., A. M. Allen, and G. Ericsson. 2016. Quantifying migration behaviour using net squared displacement approach: clarifications and caveats. PLoS One 11: e0149594. doi:10.1371/journal.pone.0149594

Smith, C., J. Meikle, and C. Roots. 2004. 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.

Sponheimer, M., T. Robinson, L. Ayliffe, B. Passey, B. Roeder, L. Shipley, E. Lopez, T. Cerling, D. Dearing, and J. Ehleringer. 2003a. An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores. Canadian Journal of Zoology 81: 871–876. doi:10.1139/z03-066

_____, _____, _____, B. Roeder, J. Hammer, B. Passey, A. West, T. Cerling, D. Dearing, and J. Ehleringer. 2003b. Nitrogen isotopes in mammalian herbivores: hair δ15N values from a controlled feeding study. International Journal of Osteoarchaeology 13: 80–87. doi:10.1002/oa.655

Tape, K. D., D. D. Gustine, R. W. Ruess, L. G. Adams, and J. A. Clark. 2016. Range expansion of moose in Arctic

Alaska linked to warming and increased shrub habitat. PLoS One 11: e0152636. doi:10.1371/journal.pone.0152636

Telfer, E. S. 1984. Circumpolar distribution and habitat requirements of moose (*Alces alces*). Pages 145–182 *in* R. Olson, R. Hastings, and F. Geddes, editors. Northern Ecology and Resource Management. University of Alberta Press, Edmonton, Alberta, Canada.

_____, and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology 65: 1828–1834. doi:10.2307/1937779

Thompson, I. D., and M. F. Vukelich. 1981. Use of logged habitats in winter by moose cows with calves in northeastern Ontario. Canadian Journal of Zoology 59: 2103–2114. doi:10.1139/z81-287

Timmermann, H. R., and J. G. McNicol. 1988. Moose habitat needs. The Forestry Chronicle 64: 238–245. doi:10.5558/tfc64238-3

Tischler, K. B. 2004. Aquatic plant nutritional quality and contribution to moose diet at Isle Royale National Park. M. S. thesis. Michigan Technologial Institute, Houghton, MI, USA.

Turner, K. W., B. B. Wolfe, and T. W. D. Edwards. 2010. Characterizing the role of hydrological processes on lake water balances in the Old Crow Flats, Yukon Territory, Canada, using water isotope tracers. Journal of Hydrology 386: 103–117. doi:10.1016/j.jhydrol.2010.03.012

_____, _____, _____, T. C. Lantz, R. I. Hall, and G. Larocque. 2014. Controls on water balance of shallow thermokarst lakes and their relations with catchment characteristics: a multi-year, landscape-scale assessment based on water isotope tracers and remote sensing in Old Crow Flats, Yukon (Canada). Global Change Biology 20: 1585–1603. doi:10.1111/gcb.12465

TWGMC (Technical Working Group and Management Committee). 2006. Old Crow Flats Van Tat K'atr'anahtii Special Management Area Management Plan. Vuntut Gwitchin Government and Yukon Environment, Old Crow, Yukon, Canada. http://www.env.gov.yk.ca/publications-maps/documents/old_crow_flats.pdf (accessed September 2019).

Van Ballenberghe, V. 1977. Migratory behavior of moose in southcentral Alaska. Transactions of the 13th International Congress of Game Biologists 13: 103–109.

_____, and J. M. Peek. 1971. Radiotelemetry studies of moose in northeastern Minnesota. Journal of Wildlife Management 35: 63–71. doi:10.2307/3799872

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. doi:10.1111/j.1365-2656.2011.01829.x

_____, B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour 84: 723–735. doi:10.1016/j.anbehav.2012.06.032

Vanderklift, M. A., and S. Ponsard. 2003. Sources of variation in consumer-diet δ 15 N enrichment: a meta-analysis. Oecologia136: 169–182. doi:10.1007/s00442-003-1270-z

Wald, E. J., and R. M. Nielson. 2014. Estimating moose abundance in linear subarctic habitats in low snow conditions with distance sampling and a Kernel estimator. Alces 50: 133–158.

Wattles, D. W., and S. DeStefano. 2011. Status and management of moose in the northeastern United States. Alces 47: 53–68.

White, K. S., N. L. Barten, S. Crouse, and J. Crouse. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95: 225–237. doi:10.1890/13-0054.1

Wolfe, B. B., M. M. Humphries, M. F. Pisaric, A. M. Balasubramaniam, C. R. Burn, L. Chan, D. Cooley, D. G. Froese, S. Graupe, and R. I. Hall. 2011. Environmental change and traditional use of the Old Crow Flats in northern Canada: an IPY opportunity to meet the challenges of the new northern research paradigm. Arctic 64: 127. doi:10.14430/arctic4092

_____, and K. W. Turner. 2008. Near-record precipitation causes rapid drainage of Zelma Lake, Old Crow Flats, Northern Yukon Territory. Meridian - Spring Edition: 7–12.

Wood, S. N. 2017. Mixed GAM computation vehicle with automatic smoothness estimation. R package version 291.