SUMMER HABITAT SELECTION BY MOOSE ON THE OLD CROW FLATS

A REPORT ON THE MOOSE COMPONENT OF YEENDOO NANH NAKHWEENJIT K'ATR'AHANAHTYAA; ENVIRONMENTAL CHANGE AND TRADITIONAL USE OF THE OLD CROW FLATS

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Summary

- Waterbodies are undergoing notable changes in the Old Crow Flats (OCF) region of Yukon, with more lakes draining or drying up than historically observed. The effects of these changes on moose presence and use in the area are currently unknown and of interest to local communities who rely on moose for subsistence. We investigated moose resource selection in the OCF to predict the future consequences of changing lake systems on moose habitat and to inform moose management and conservation measures.
- A habitat selection analysis for moose in the OCF during the summer months (i.e., open water, May 15 to October 1) was conducted. To identify the factors that influenced moose habitat selection within an individual's home range, habitat selection was modeled at a local scale (i.e. 3rd order) using 9,069 observations from 14 moose (7 male and 7 female) over 3 years (2007 to 2009). Individual moose models were averaged to produce a habitat selection model for the "average" moose in the flats. For all models, a resource selection function (RSF) was fitted which considered a set of variables describing habitat that were hypothesized to be important to moose. Variables describing habitat features across the study area were derived from a land cover classification map developed using remotely sensed data.
- In the OCF during the summer, individual moose were remarkably uniform in their habitat selection patterns at the local scale assessed. A typical moose was more likely to use areas closer to water, with a greater proportion of upright shrub, and a higher diversity of vegetation types in the vicinity. This pattern corresponded well with a previous stable isotope analysis of moose diets in the OCF area.
- Only two moose had sufficient data to assess the influence of drained lakes and fluctuating lakes on habitat selection. For those moose, although drained and fluctuating lakes did not greatly influence the models, these habitats positively affected site selection. However, the sample size was too small to draw population-level conclusions about drained and fluctuating lake selection within home ranges.

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Introduction

The Old Crow Flats (OCF) is a highly important wetland and lake complex. It provides habitat for large populations of waterfowl and shorebirds, as well as the Porcupine caribou herd, muskrat, fish, and moose. The OCF represents the study area for a large inter-disciplinary ecological study by numerous academic researchers, led by the Vuntut Gwitchin First Nation and funded by the Canadian International Polar Year program. The project is titled Yeendoo Nanh Nakhweenjit K'atr'ahanahtyaa; Environmental Change and Traditional Use of the Old Crow Flats (YNNK).

The project was developed in response to local concerns that water levels in the OCF are changing and that more lakes are draining or drying up (Wolfe et al. 2011; Arctic Borderlands Ecological Knowledge Coop 2007). The broad objectives of the overall YNNK project were to examine how climate and the OCF have changed over the past several thousand years and how climate change might affect the OCF in the future (Vuntut Gwitchin First Nation 2006). A significant component of the project was to study the traditional food sources of the Vuntut Gwitchin people and develop an adaptation plan for the future. The development of long-term environmental monitoring protocols for the OCF was also a long-term goal.

Moose (*Alces alces gigas*) are an important food source for the Vuntut Gwitchin people and represent a large component of the YNNK study. Local knowledge and past resource

inventory work indicated that moose were very numerous in the OCF in summer but were virtually absent throughout much of the winter (Government of Yukon, pers. comm.). Summer waterfowl transect surveys in the OCF in the mid-1970's recorded moose at low densities and reported seasonal differences in moose abundance. At the time, moose densities in the OCF ranged from 85 to 185 moose per 1,000 km² (Mossop 1975). Currently, moose density in the OCF is assumed to be lower than the Yukon average of 158 moose per 1,000 km² (Czetwertynski et al. 2012; Yukon Fish and Wildlife Branch 1997, 2003).

A five-year moose collaring study conducted in the late 1990's by the U.S. Fish and Wildlife Service, in the Arctic National Wildlife Refuge (ANWR) showed that most moose captured on winter ranges in Alaska migrate up to 250 kilometres to spend the summer in the western half of the OCF and return to the same winter ranges in fall (Mauer 1998). Additional examination of the ANWR location data indicated that all moose displaying migratory behaviour did so every year. Most migrants arrived in the OCF by early May, just before spring break-up, and most departed in August and September, prior to the rut and before temperatures declined with the onset of winter (Yukon Fish and Wildlife Branch 2007b).

To determine the contribution of aquatic and terrestrial vegetation to moose diet in the summer, Milligan (2010) conducted a stable isotope analysis. This stable isotope project was further informed by a study on the changes in aquatic plant abundance and nutrient content

throughout the year in the OCF to better understand the nutritional composition of moose food plants over the summer (Humphries et al. 2010).

The stable isotope analysis showed that the proportion of aquatic vegetation in the diet increased from 3% to 14% as late-winter progressed into spring, and then summer (Milligan 2010). Furthermore, aquatic vegetation appeared more important for male moose than female moose and for those moose occupying lake habitats, and/or the southern end of the OCF. In addition, several past fecal analysis studies have indicated that moose feed on terrestrial forbs and shrubs year-round with the consumption of freshwater aquatic plants peaking in the spring or early summer (Franzmann and Schwartz 2007; Fraser et al. 1980; Fraser et al. 1982; Van Ballenberghe et al. 1989).

The objective for the moose component of YNNK was to examine habitat use and selection, and to predict how changing water levels may affect moose and moose habitat, within the OCF. Moose likely favour drained lake basins with an abundance of shrubs, however they also use aquatic habitats (MacCracken et al. 1997). When lake water levels drop, as predicted with climate change (Prowse et al. 2006), vegetation shifts from aquatic to terrestrial species such as willow; thus, there is a need to understand how important each type of food is to moose to help understand the potential effects of a changing climate. The use of habitat selection modeling for the OCF is an effective way to meet the study objective as selection models can identify the relationship between a diversity of variables of

interest (e.g. shrubs, open water, etc.) and the probability of use by a moose.

This report details the resource selection and habitat suitability analysis for moose in the OCF in the summer months. Because the stable isotope analysis indicated that moose diets are comprised primarily of terrestrial rather than aquatic vegetation, and that the degree of this can vary depending on local habitat conditions and sex, individual moose were modeled to specifically compare the relative level of use of aquatic and terrestrial habitat within each moose's home range. This also provided information on the amount of diversity in habitat selection across the OCF landscape. Drained and fluctuating lake basins were relatively rare within the home ranges of the moose analysed and as such, the majority of models focused more generally on the suitability of different vegetated land cover types and the distance to aquatic features. To understand habitat suitability for an "average" moose in the OCF, a habitat selection model was developed by averaging models across all individual moose.

Methods

Study Area

The study area is part of the Old Crow Flats Ecoregion and is situated within Vuntut National Park and the Old Crow Flats Special Management Area (Figure 1). There are approximately 9,000 lakes and small ponds in the area that represent approximately 30% of the 5,600 km² area (Turner et al. 2010).

The regional climate in the OCF is continental and is characterized by cold winters (mean January temperature of -31.1°C) and warm summers (mean July temperature of 14.6°C). Mean annual precipitation measured at the Old Crow Airport is 266 mm, with slightly less than half of this classified as snowfall (Turner et al. 2010). The landscape is a mosaic of terrestrial, riparian and aquatic environments that provide abundant

habitat for muskrat, moose, fish, and hundreds of thousands of migratory birds (Smith et al. 2004). Local relief is very small and water covers approximately 35% of the area. Permafrost features, such as, ice wedge polygons and retrogressive thaw slumps, are relatively common. The Old Crow River is a shallow river that drains through the study area and into the Porcupine River to the south (Smith et al. 2004).

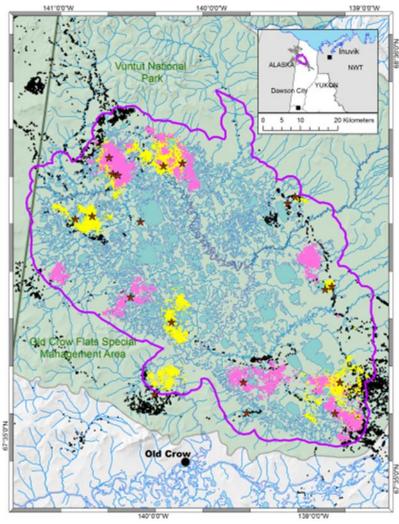


Figure 1. Map of the Old Crow Flats study area. The yellow and pink dots represent male and female moose locations, respectively, used for habitat selection modeling. The black dots represent locations that were excluded from the analysis (see Methods). The red stars represent the July and August 2007 capture locations. The purple polygon shows the extent of the land cover classification used in the model.

The vegetation in the OCF is a mosaic of upright shrub and dwarf shrub tundra, and spruce woodlands. Shrub tundra is found throughout the OCF, while spruce woodlands are most common adjacent to major rivers and creeks and on some south facing slopes. Sedge wetlands and peatlands are also found throughout the region and shallow lakes are frequently dominated by visible aquatic plants. Drained lake basins and fluctuating lake shorelines are dominated by a mix of dense willow thickets and sedge wetland. Sparsely-vegetated areas are common at high elevations and adjacent to creeks and rivers.

Moose Location Data

Satellite GPS collars (GPS 4400MTM, Lotek, Newmarket, Ontario) were deployed on 10 adult male and 9 adult female moose between 31 July and 4 August, 2007. Moose capture locations were selected to reflect moose density and distribution observed during a pre-capture flight (Yukon Fish and Wildlife Branch 2007a). In most cases, 1 male and 1 female moose were captured in the same general area (Figure 1).

GPS collars were programmed to record locations either every 5 hours (16 collars) or every 4 hours (3 collars). Using the known transmission schedule, the number of locations was summarized for each moose to identify any 'missed' locations. Missed locations may occur, for example, as a result of immersion in water which prevents the collar from recording a location (Yukon Fish and Wildlife Branch 2009). The number of missed locations was less than 5% of all locations and thus

there was no need to investigate or control for their effect in the habitat selection model (Neilson et al. 2009).

Locations recorded within 72 hours of capture in 2007 were excluded from the analyses so as to remove any behavioural effects of capture. All location data that was 2D (2dimensional; 2D data is less accurate than 3D (3-dimensional) or had a PDOP value greater than 10, were also excluded from the analyses (Dussault et al. 2001). The PDOP, or the "Position Dilution of Precision", indicates the precision of a location. The lower the value, the better precision a location has and thus, likely a more accurate position. Locations that fell outside of the area covered by the land cover classification used in the model were also excluded.

To limit the habitat selection analysis to the OCF during the summer, only moose locations that occurred between May 15 and October 1 of each year were used. These dates were chosen to represent the summer season as they indicate the start, and end, respectively, of the probable ice-free season in the OCF (http://weather.gc.ca/).

Five moose did not have a full summer season of location data in the OCF (3 moose died and 2 collars failed) and thus, these individuals were excluded from the analyses. Of the 14 moose retained for the study, 10 collars were recovered at the completion of the study period and the internal data stored on them were downloaded. For the remaining four collars, only the transmitted data were used in the analysis. The satellite uplink had been scheduled so that all data within the collar's memory buffer

would be transmitted as opposed to transmitting only a portion of the stored data. Therefore, transmitted data were assumed to include all data points collected by that collar.

No telemetry flights were flown during the study so it is unknown whether female moose had calves at any point other than during the two capture sessions. There were two females with calves at heel during the initial captures in 2007 and 2 females with calves at heel during the recapture in 2009 to remove the collars.

Land Cover Model Variables

A land cover classification was created to include terrestrial and aquatic variables in the habitat selection models. The map was developed using two satellite images from two different dates during the peak of the 2008 growing season (July 23rd and August 10th). Individual images were histogram matched and mosaicked in ENVI (ENVI 2006) by selecting ground control points on a georeferenced panchromatic SPOT image provided by the image vendor: Alberta Terrestrial Imaging Centre. To correct for any distortions in portions of the study area with greater relief, the multispectral mosaic was georeferenced again in ArcGIS using a single LandSat satellite image taken in 2008. Both georeferencing procedures were performed using a 2nd order polynomial and approximately 200 ground control points. Prior to classification, this image was clipped to study area extent as shown in Figure 1.

An object-based approach was used to create the land cover classification using the image mosaic.

This technique involves two steps: 1) segmenting the imagery into groups of pixels (i.e. objects) organized in a nested hierarchy, and 2) classifying these objects. In the software package used, segmentation is a bottom-up, region merging algorithm that generates objects that conform to user-defined shape criteria (Definiens 2006). Objects were created by minimizing the heterogeneity (colour) of successively larger groups of pixels. The process was complete when the heterogeneity of an object exceeded a threshold defined by a unitless scale parameter. Iteratively modifying the heterogeneity threshold by changing the scale parameter allows users to segment the image into objects that reflect landscape structure at multiple scales (Benz et al. 2004; Blaschke and Hay 2001; Definiens 2006). Once segmentation was completed, the objects were classified using defined membership rules (e.g., thresholds) or a nearest neighbour classifier based on training data (Laliberte et al. 2004). One of the most powerful aspects of this approach was that fine-scale objects belonging to unique objects at broader scales could be classified in separate processes (Definiens 2006).

The mosaic of the OCF was segmented at three spatial scales. To eliminate cloud cover and minimize confusion between water and dark-coloured vegetation in this lake-rich region, large image objects with borders that corresponded to the boundary between water bodies, land, and clouds, were created by segmenting the image using a scale parameter of 150. In this process, segmentation bands with a greater ability to discriminate between water

and land were given higher weighting (green=1, red=1, near infrared=10, mid infrared=10). To discriminate between turbid and clear water, a meso-scale segmentation was performed using a scale parameter of 15. This segmentation used all four bands with the following assigned weights (green=1, red=1, nearinfrared=10, mid-infrared=10). To create the fine-scale objects necessary to classify vegetation, a fine-scale segmentation was performed using a scale parameter of 12 and equal weighting of the green, red and near infrared bands. All segmentations were performed using a colour to shape ratio of 0.9 and compactness to smoothness ratio of 0.5 (Definiens 2006).

To map the land cover in the OCF, an iterative procedure was used that took advantage of the nested arrangement of broad-, meso-, and fine-scale image objects. First, coarsescale image objects were classified as land, water and cloud using a nearest neighbour classifier (NNC). Open water was distinguished from water dominated by aquatic vegetation by applying a second NNC to all objects identified as water in the first step. Clear and turbid water were distinguished from one another by applying a third NNC to the mesoscale image objects nested within the broad-scale objects that were still identified as water.

The terrestrial surface of the study area was further classified using the fine-scale image objects nested within each land object. Classes identified using a NNC included: herbaceous, upright shrubland, dwarf shrubland, woodland, peatland, and sparsely vegetated/barren (Figure 2). Fine-

scale objects nested within areas classified as clear water, turbid water, cloud or aquatic vegetation at other levels of the scale hierarchy, inherited the class membership at the coarser scale.

To select classification training areas, data from several sources collected in 2009 were used. These included ground-based vegetation surveys and oblique and vertical photographs captured during a lowelevation survey conducted in a Cessna 185. Vertical images were obtained using digital cameras mounted under each wing (Canon PowerShot S80 and Tetracam ACD). Oblique images were also obtained using a Nikon D80 operated inside the aircraft. Photographs were captured at an altitude of approximately 600 m and had pixel sizes typically less than 0.25 m. The spatial location of these images was determined using RoboGeo (Pretek Inc. 2003-2015) to interpolate points on a GPS track-log using the time that each image was captured.

To examine the accuracy of the object-based classification, a standard accuracy assessment was conducted. This involved comparing 800 ground truth points (100 per class) with the classification. Further independent validation data was obtained from the aerial surveys described above. Overall accuracy was calculated using class user and producer accuracies and the kappa statistic (Lillesand et al. 2003).

The resulting confusion matrix (Table 1) indicated that the land cover classification of the OCF had an overall accuracy of 83%. The kappa statistic which ranges from 0 to 1 and provides a measure of accuracy,

correcting for the possibility that objects are classified correctly by chance was 0.8. User and producer accuracies ranged from high (92% to 100%) for lakes and sparsely vegetated areas, to moderate and high (69% to 92%) the remaining land cover classes.

To provide a data layer that would inform the habitat selection analysis, rare vegetation classes that covered <5% of the study area were combined into a new class with other rare or similar vegetation (

Table 2).

There have been few regional wildfires (1,036 km² or ~ 6.5 % of the study area) and very few anthropogenic disturbances (212 km² or 3.8% of the study area), in the study region. These features were not considered to have had an influence on moose habitat selection, and were, therefore, excluded from the analyses.

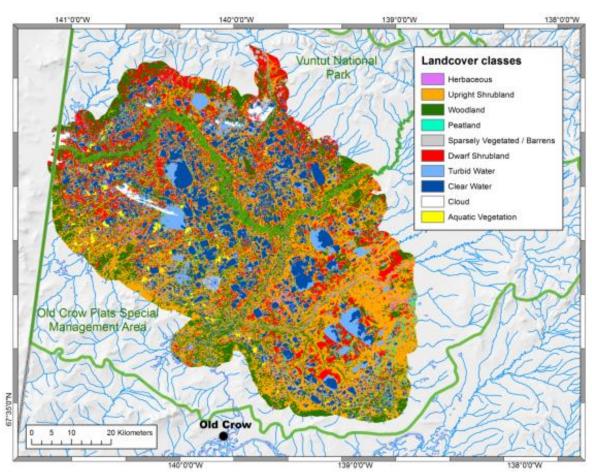


Figure 2. Land cover classification of the Old Crow Flats study area.

Table 1. Confusion matrix resulting from an accuracy assessment of the object-based land cover classification of the Old Crow Flats. The table shows tallies, producer and user accuracies, overall accuracy, and the kappa coefficient.

| Reference Data → ↓ Classified Data | НВ | SL | WL | PL | υv | DS | TW | cw | AV | Total | User Accuracy (%) |
|------------------------------------|-----|-----|----|----|----|-----|-----|-----|----|-------|-------------------------|
| Herbaceous | 55 | 16 | 1 | 3 | 0 | 0 | 3 | 0 | 2 | 80 | 69 |
| Upright Shrubland | 13 | 97 | 11 | 0 | 0 | 4 | 1 | 0 | 0 | 126 | 77 |
| Woodland | 0 | 5 | 70 | 0 | 4 | 8 | 2 | 0 | 0 | 89 | 79 |
| Peatland | 2 | 3 | 0 | 78 | 1 | 15 | 0 | 0 | 0 | 99 | 79 |
| Sparsely Vegetated | 0 | 0 | 0 | 0 | 76 | 0 | 0 | 0 | 0 | 76 | 100 |
| /Barren | | | | | | | | | | | |
| Dwarf Shrubland | 0 | 11 | 9 | 4 | 1 | 84 | 2 | 0 | 0 | 111 | 76 |
| Turbid Water | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 100 | 100 |
| Clear Water | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 94 | 3 | 98 | 96 |
| Aquatic Vegetation | 1 | 3 | 1 | 0 | 0 | 0 | 15 | 8 | 94 | 122 | 77 |
| Total | 71 | 135 | 92 | 85 | 82 | 111 | 124 | 102 | 99 | 901 | |
| Producers Accuracy (%) | 77 | 72 | 76 | 92 | 93 | 76 | 81 | 92 | 95 | | |
| Overall Accuracy (%) | 83 | | | | | | | | | | |
| Карра | 0.8 | | | | | | | | | | |

Table 2. Definitions of land cover classes, their abundance on the landscape, and whether they were combined with other classes for the purposes of habitat selection modeling.

| Vegetation class | Description | Total area covered (km²) | % of study area | Combined |
|---------------------------|---|-----------------------------|-----------------------|---------------------------|
| Aquatic veg | Shallow waterbodies dominated by visible plants | 41 | 0.8 | No |
| All water | Clear water and Turbid water classes combined | 1190 | 21.7 | No |
| Upright shrub | Terrain dominated by woody vegetation > 40 cm | 1860 | 33.9 | No |
| Woodland | Terrain characterized by open spruce woodlands | 1061 | 19.3 | No |
| Open terrain | Peatland + Herbaceous + Dwarf Shrub | 1238 | 22.6 | No |
| Sparsely vegetated/barren | Unvegetated surfaces (talus, sandbars, etc.) | 100 | 1.8 | No |
| Peatland | Areas dominated by peat forming mosses | 222 | 4.0 | Yes (see Open terrain) |
| Herbaceous | Areas dominated by <i>Carex</i> spp. and <i>Eriophorum</i> spp. including tussock tundra and sedge wetlands | 154 | 2.8 | Yes (see Open terrain) |
| Dwarf shrub | Terrain dominated by woody vegetation < 40 cm | 861 | 15.7 | Yes (see Open Terrain) |

Waterbody Condition Model Variables

Data from Lantz and Turner (2015) were used to include information on the condition of waterbodies in the study area. Lantz and Turner (2015) used grayscale air photos from the National Library of Canada (1951, 1952 and 1972), LANDSAT images (1973 – 2010), and SPOT5 imagery (2007) to identify lakes that exhibited large changes in area between 1951 and 2010. Subsequently, they used annual estimates of lake area derived from the Landsat archive to classify lakes into one of the following four groups:

1. Catastrophic drainages:

Decreases in lake area ≥30% occurring between subsequent images (e.g., 1981–1982), with an increase in area not ≥30% over the remainder of the data record

2. **Large fluctuations**: decrease in lake area ≥30% occurring between subsequent images.

- 3. **Gradual-cumulative** declines:

 Decrease in lake area ≥30% over the entire record resulting from cumulative annual losses in area.
- 4. **No threshold change:** No increase or decrease in lake area ≥30% between subsequent images or over the entire period of record.

To provide additional information for the habitat selection models we used these data to classify lakes as either "drained" or "fluctuating". Drained lakes included those which showed an overall decrease in area ≥30%. Fluctuating lakes included those which showed an overall increase or decrease in area ≥30% followed by a decrease or increase in area ≥30%, respectively. Finally, the land cover classification was updated by merging the clear and turbid water classes and updating the status of lakes classified as drained or fluctuating. The remainder of the image was classified as land (

Table 3, Figure 3).

Table 3. Description of final waterbody condition classes in the Old Crow Flats study area and their abundance on the landscape.

| Lake Class | Description | Total area covered (km²) | % of study area |
|------------------|---|--------------------------------|--------------------|
| Drained lake | Decrease in lake area ≥ 30% over the entire record, resulting from abrupt or cumulative losses in area. | 50 | 1.0 |
| Fluctuating lake | Increase or decrease in lake area ≥ 30% followed by a decrease or increase ≥ 30% (respectively). | 16 | 0.3 |
| Open water | Clear water and turbid water classes combined | 1,156 | 21.7 |
| Land | Remainder of the image | 4,104 | 77.0 |

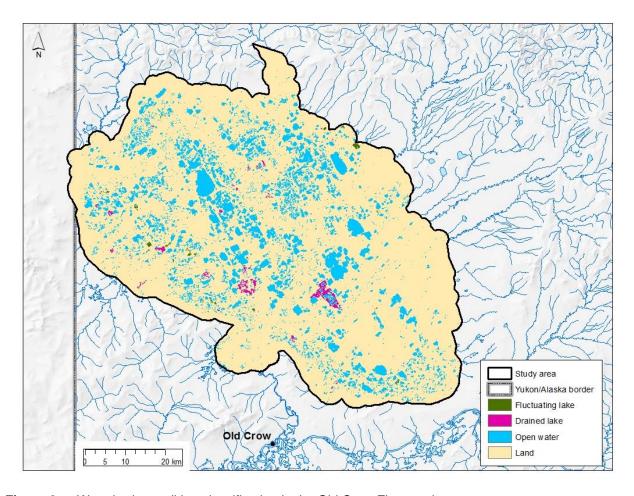


Figure 3. Waterbody condition classification in the Old Crow Flats study area.

Topographic Model Variables

At the latitude of the OCF, moose very rarely use elevations above 900 metres during the summer (Smits 1991); however, no part of the study area exceeded this elevation and thus there was no need to exclude areas from the analysis based on elevation. Similarly, the range of elevations between used and random points was very small and the measurements of slope and aspect were non-informative. This resulted in the exclusion of any topographic variables (e.g. elevation, slope, aspect, topographic position) that are often

used in moose habitat selection modelling.

Model Variable Selection

Although a range of biophysical variables were considered for use in developing the habitat selection models, it was necessary to eliminate some of them prior to the creation of the candidate model set.

Aquatic vegetation is rare on the landscape (

Table **2**), and thus, this land cover class was dropped from the analyses for all moose. One of the original goals of this study was to test the influence

of drained and fluctuating lakes on moose habitat use and selection. Unfortunately, these aquatic features are also rare on the landscape (Table 3), and used and random locations were not typically situated within them often enough to provide sufficient data for the models. Consequently the influence of these features on habitat selection could be assessed for only two of the 14 moose. For these two moose, the proportion of drained or fluctuating lakes within a 100 metre radius of each used or available point was assessed.

To provide a more general sense of the use of drained and fluctuating lakes by moose, the proportion of collar locations occurring in each class was calculated for each study year and each sex. These values were related to those of the open water and land classes to identify patterns of relative use among four major classes. It is important to recognize that because this additional analysis did not discriminate among individual moose, results indicate the use of these habitats in only a very general sense.

Following exclusion of the above aquatic feature variables, the following variables were included in the complete set of candidate models: the distance to water; the squared value for distance to water (to account for selection or avoidance of midrange distances); diversity (i.e. the number of individual landcover vegetation classes present); and the proportions of upright shrubs, woodland, and open terrain habitats. All variables (other than the distance to water) were measured within a 100 metre radius of each used and available point.

Resource Selection Functions

Habitat selection was modeled using resource selection functions (RSFs). RSFs use characteristics of samples of used and available resource units to provide values for resource units that are proportional to their probability of being used by the study organism. Exponential RSFs were used, which took the form:

$$W(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \dots + \beta_i x_i)$$

where W(x) is the RSF, x_1 is the value of the i_{th} biophysical variable for each considered resource unit, and β_1 is the coefficient value assigned to the i_{th} biophysical variable for each considered resource unit (Manly et al. 2002). Coefficient values are estimated using logistic regression.

Conditional logistic regression was used to examine resource selection by moose within their home range (i.e. third-order; Johnson 1980). Conditional logistic regression matches particular available or unused points with particular known or used points along an animal's movement path, where resources are being selected. This matched-case control design examines selection along a restricted area (i.e. movement path) rather than the entire landscape (Compton et al. 2002). Five available points were generated for each used point, and were selected randomly within a buffer around the used point. Buffers were developed using ArcGIS 10.0 spatial analyst and had a radius equal to the distance to the next location along the movement path of the moose also known as the step length. The buffer area thus represents where a moose could have

potentially travelled between the first location (i.e. the used point) and the next location. Using this approach ensures that, as in reality, the resources available to an individual moose change with each successive step or location. Where a portion of a buffer fell outside the study area, the buffer was clipped to the study area and available points were randomly selected only within the remaining portion.

This method also assumes that availability depends on the behaviour of individual moose. Although mixed-effect conditional logistic regression with each individual animal treated as a random effect can be used, it is challenging and often leads to complicated interpretations of the models (Gillies et al. 2006; Knopff et al. 2014). Instead, a "two-step modeling approach", which applies model selection for each individual moose followed by the averaging of variable coefficients from each individual moose model to obtain the

coefficient values for the population model (Fieberg et al. 2010; Knopff et al. 2014) was used. In this analysis each individual was weighted equally when the coefficients were averaged to derive the population-level habitat selection model for the OCF moose.

Model Selection

Seven a-priori models were developed which represented all total combinations of the variables of interest (i.e. those factors hypothesized to be driving habitat selection within the home ranges of OCF moose; (Table 4). All variables used were considered to be biologically important based on previous studies and observations of moose in this region (Milligan 2010: Dussault et al. 2006; Dungan and Wright 2005; MacCracken et al. 1997; Van Ballenberghe et al. 1989). Home ranges were estimated using a kernel density method.

Table 4. Candidate model set based on habitat components hypothesized to be important to moose during summer in the Old Crow Flats, Yukon. All vegetation variables represent the proportion of area covered within a 100m radius.

| Model # | Variables |
|---------|--|
| 1 | Distance to water + Distance to water ² |
| 2 | Diversity |
| 3 | Woodland + Upright shrub + Open terrain |
| 4 | Distance to water + Distance to water ² + Diversity |
| 5 | Diversity + Woodland + Upright shrub + Open terrain |
| 6 | Distance to water + Distance to water ² + Woodland + Upright shrub + Open terrain |
| 7 | Distance to water + Distance to water ² + Woodland + Upright shrub + Open terrain + Diversity |

As previously mentioned, biophysical variables that were rare overall across the study area were not included in the candidate models. However, to specifically examine the influence of waterbody condition on moose habitat selection, two rare waterbody condition variables (i.e. fluctuating lake and drained lake) were included in a separate set of apriori models for two home ranges (home range sections 2 and 5) in which these variables were sufficiently abundant for analysis. The results from this separate model selection exercise are described in the results and discussion. For every used and available point location, a z-score transformation $(|x - \bar{x}|/\sigma_x)$ was used to standardize the values of all the continuous variables included in the analysis (Northrup et al. 2013). This allowed for the interpretation of the relative influence of each variable in the RSF model (Knopff et al. 2014). In addition, all variables were screened for collinearity using Pearson's Correlations (r; Zar 1999). Correlations in which |r| > 0.70 were deemed to be collinear, except in the case of quadratic terms, which were expected to be highly correlated with their parent term. In cases of collinearity, the variable that either: 1) increased model parsimony (i.e., excluded the variable with a squared term), 2) was deemed to be more interpretable, or 3) had the lower AIC value for the single variable logistic regression model, was selected for use. The other variables were no longer considered in the models.

For each candidate model, RSF coefficients were estimated using conditional logistic regression in *R*

statistical software (R Development Core Team 2015). Candidate models were ranked for each moose home range using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). The population-level model was identified as that with the highest average AIC weight (w_i) among all candidate models. Model coefficients were estimated by averaging the coefficients generated for that model from each home range. Population-level coefficients with confidence intervals which did not overlap zero indicated regular patterns of use (Knopff et al. 2014).

Model Validation

The top-ranked population-level model was validated using k-fold cross-validation (Boyce et al. 2002). For each home range, matched casecontrol sets were randomly divided into five subsets (i.e., k=5) to eliminate any possible individual bias in the creation of the subsets. Each data subset was then used as a validation sample for RSFs created using data from the remaining four subsets. Each cross-validated model was applied to the landscape in ArcGIS 10.0 and bin sizes based on the quantiles of the predicted RSF values were developed. Frequencies of used locations from the validation datasets were then binned according to their RSF value and they were adjusted to the proportion of the study area that was bounded by the predicted RSF values for each bin (Boyce et al. 2002). Area-adjusted frequencies below 1.0 would indicate that used locations occurred at rates less than expected, while values greater than one would indicate that used locations

occurred at rates greater than expected given the available area of that range of RSF score within the landscape. A Spearman's rank (r_s) correlation was used to compare the RSF bins to the area-adjusted frequencies of used locations within each bin for each validation subset. A positive and significant Spearman rank correlation between bin rank and area-adjusted frequency rank denote a model with good predictive performance (Zar 1999).

Results

Location Data

A total of 19 adult moose were captured and fitted with radio-collars; 14 of these individuals (7 male and 7 female) provided data for the analysis. Location data were screened to include only points recorded during the summer growing season (May 15 to October 1), resulting in 9,069 locations (4,993 for females and 4,076 for males). The mean number of locations per moose was 647 and varied considerably from 62 to 931.

While most individual moose established a single distinct home range during the study period, three moose each used two distinct and separate areas. To account for the behavioural differences of these moose relative to the others, each were considered to have two separate home

ranges. These ranges were analysed independently from one another and were termed 'Home Range Sections' (HRS). To be consistent, all other home ranges were also referred to as HRS. For one moose, (HRS 15), the set of candidate models could not be evaluated due to limited data, thus reducing the number of evaluated HRS to 16 (Fig. 4 and 5).

Variable Screening

For each HRS, only uncorrelated variables were used in the models, ensuring they were independent of one another. Because it was only possible to include waterbody condition variables (i.e. drained lake and fluctuating lake) in two of the HRS, a set of candidate models for all HRS that did not include these variables was created. Subsequently, a second set of candidate models for HRS 2 and 5 including water condition variables was created. This allowed for the comparison among as many moose with a similar set of variables as possible, while also providing information on the importance of drained and fluctuating lakes in moose habitat selection.

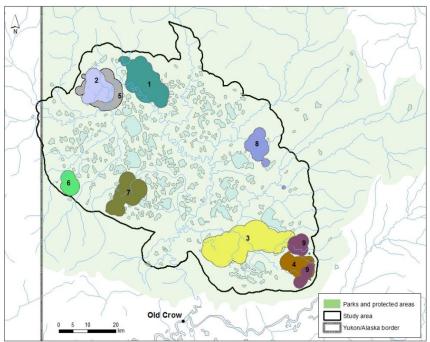


Figure 4. Locations of Home Range Sections (HRS) 1-9 for adult female moose that were analysed in the study. HRS number is indicated for reference (Table 4). Colors are used only to clarify boundaries among sections. Note: HRS 9 is a single home range but is split into two areas due to two distinct areas of concentrated use within the range with a travel corridor connecting them.

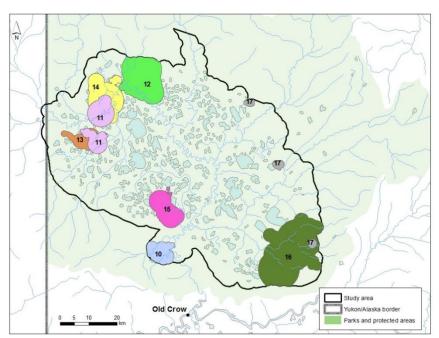


Figure 5. Locations of Home Range Sections (HRS) 10-17 for adult male moose that were analysed in the study. HRS number is indicated for reference (Table 5). Colors are used only to clarify boundaries among sections. Note that HRS 15 did not have sufficient data for analysis and was excluded. HRS 11 and HRS 17 are considered single home ranges but each is split into multiple areas due to distinct areas of concentrated use within each range with travel corridors connecting them.

Table 5. Akaike weights (wi) for each candidate model by home range section (HRS) for moose collared in the Old Crow Flats, Yukon, during summer. HRS 15 did not have sufficient data to evaluate the candidate models and was not analysed. AIC weights in bold text indicate the top-ranked model for each HRS.

| | | | AIC weights (w _i) for Home Range Sections (HRS) | | | | | | | | | | | | | | | |
|-------|---|-------|---|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-----|-------|-------|
| Model | Components | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| 1 | Distance to water + Distance to water ² | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.095 | 0.000 | 0.000 | 0.135 | 0.003 | 0.000 | 0.000 | 0.000 | 0.000 | n/a | 0.000 | 0.000 |
| 2 | Diversity | 0.000 | 0.000 | 0.000 | 0.000 | 0.002 | 0.129 | 0.000 | 0.000 | 0.317 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | n/a | 0.000 | 0.276 |
| 3 | Upright shrub + Open terrain + woodland | 0.013 | 0.000 | 0.001 | 0.000 | 0.000 | 0.008 | 0.000 | 0.000 | 0.108 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 | n/a | 0.000 | 0.000 |
| 4 | Distance to water + Distance to water ² + Diversity | 0.000 | 0.000 | 0.000 | 0.000 | 0.001 | 0.105 | 0.557 | 0.000 | 0.087 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 | n/a | 0.000 | 0.048 |
| 5 | Diversity + Upright shrub + Open terrain + Woodland | 0.557 | 0.009 | 0.314 | 0.000 | 0.122 | 0.281 | 0.000 | 0.000 | 0.252 | 0.005 | 0.025 | 0.000 | 0.000 | 0.000 | n/a | 0.003 | 0.162 |
| 6 | Distance to water + Distance to water ² + Upright shrub + Open terrain + Woodland | 0.059 | 0.027 | 0.012 | 0.001 | 0.000 | 0.077 | 0.000 | 0.000 | 0.030 | 0.590 | 0.000 | 0.000 | 0.000 | 0.000 | n/a | 0.020 | 0.004 |
| 7 | Distance to water + Distance to water ² + Diversity + Upright shrub + Open terrain + Woodland | 0.371 | 0.964 | 0.674 | 0.999 | 0.874 | 0.305 | 0.443 | 1.000 | 0.071 | 0.399 | 0.974 | 1.000 | 1.000 | 1.000 | n/a | 0.977 | 0.510 |

Model Selection per Moose

Candidate models were evaluated separately for each of the 16 moose HRS (Table 4). In general, the models explained only a small portion of the deviance in the data (typically <10%). This indicates a relatively poor model fit and suggests that there are other important factors, not captured in the models assessed, which are more strongly affecting habitat selection.

A model's beta coefficients indicate the direction of the relationship between the variable and the probability of a location being used (i.e., selection or avoidance). Overall, the model selection results for all 16 home range sections were remarkably similar (Appendix A). Model 7 was the top model (i.e., best supported by the data) in 12 of the 16 HRS, and had 'substantial support' in three of the other four HRS. In other words, Model 7 was either ranked first or second in 15 out of 16 HRS (Table 4). This model indicated that in general, the use of a given site within a home range was best predicted by an intermediate distance from water (indicated by a negative quadratic relationship), high landcover diversity, and a high abundance of upright shrub, open terrain, and woodland; however, some exceptions exist (see Appendix A). Mapped results of the top model for each individual moose HRS are shown in Appendix B.

One moose (HRS 9) showed a different pattern of site use from the

others, with its top model indicating that the probability of a site being used was greater in areas with higher levels of vegetation diversity only. However, there were other strongly supported models (Models 1 and 5) for that HRS which suggested that site selection is also influenced by the proximity to water, and the amount of woodland, upright shrub and open terrain (Table 5).

Model Averaging

The top models from each of the 16 individual HRS were combined using a model averaging procedure to create a single, population-level model that represents the habitat selection of an 'average' moose (Table 6). This model indicated that moose were more likely to use locations that were a) an intermediate distance from water (i.e. close, but not directly adjacent), b) had a higher amount of upright shrubs, woodland, and open terrain, and c) had a higher diversity of vegetation types, than other locations. In other words, moose were selecting areas in close proximity to water (695 metres was the quadratic term minima, or the distance of strongest selection against water), with a variety of vegetation types in the surrounding 100 metres. It should be noted that the variables with the greatest influence on the model were the distance to water and the proportion of upright shrubs. These variables had the two largest coefficients.

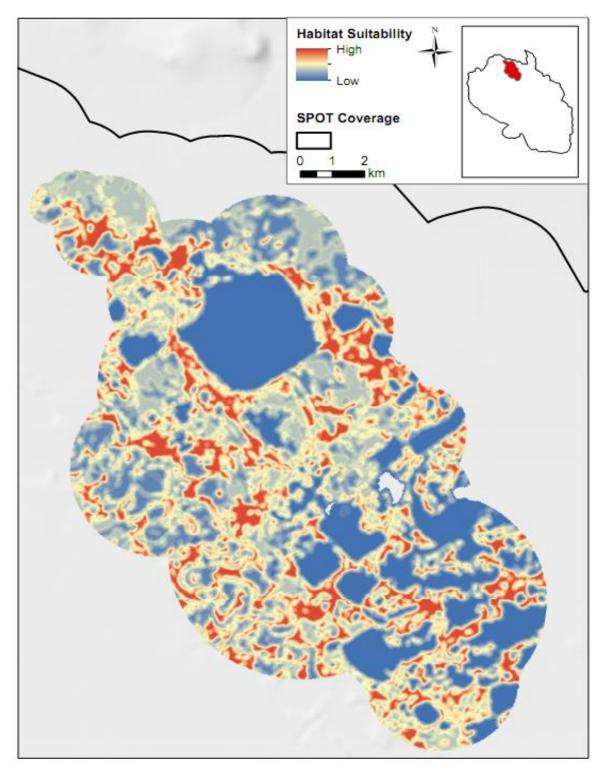


Figure 6. Example of mapped model results depicting relative habitat suitability for moose in summer in a single home range section (HRS1). Mapped model results for all individual moose HRSs are shown in Appendix B.

The Effect of Waterbody Condition

For the two HRS where the influence of drained lakes and fluctuating lakes could be evaluated using RSF models (HRS 2 and 5), the results indicated the strongest support for Model W15 (Table 7; Appendix A). In both cases, the probability of a location being used increased with the proportion of drained or fluctuating lake present within a 100m radius. Overall, models for both HRS 2 and HRS 5 indicated that the probability of a location being used was affected by both of the lake variables, as well as distance to water; diversity; and the amount of upright shrub, open terrain, and woodland (Table 7). The differences in covariate values for each waterbody condition variable between the two home ranges modeled (HRS 2 vs. HRS 5), suggests

that the strength of this effect on habitat selection varies with moose and/or home range condition. Additional data from more individual moose in areas where drained and fluctuating lakes are more abundant are required to fully evaluate and extrapolate these relationships. The broad-scale analysis on waterbody condition which compared the proportion of use among four broad landcover classes (Table 3) indicated that overall, land was used most often, followed by open water, fluctuating lakes, and drained lakes (Table 8). However, when the proportion of use in each class was related to the proportion of the study area covered by each class, the results provided tentative support to the hypothesis that drained and fluctuating lakes may be selected by moose (Figure 7).

Table 6. Beta coefficients (β) and 95% confidence intervals for the variables included in the model developed through the averaging procedure that created a model representing an average moose.

| Covariate | β | 95 % Confiden | ce Interval |
|--------------------------------|--------|---------------|-------------|
| | | Lower | Upper |
| Distance to water | -1.089 | -1.771 | -0.408 |
| Distance to water ² | 0.301 | -0.123 | 0.724 |
| Upright shrub | 0.583 | 0.272 | 0.895 |
| Diversity | 0.295 | 0.099 | 0.491 |
| Woodland | 0.213 | -0.292 | 0.718 |
| Open terrain | 0.099 | -0.391 | 0.590 |

Overall, moose appeared to use fluctuating lakes more than expected given moose abundance on the landscape (Figure 7). However, when looking at results by sex or year, some trends emerged suggesting that use (and possible selection) is related to moose behaviour and/or annual conditions. Specifically, the use of drained lakes was much higher by females than males for only 2007 and 2009, while the use of fluctuating

lakes was much higher by males than females for 2008 and 2009. Over the three study years, the use of drained lakes by both males and females decreased, while their use of fluctuating lakes increased. Neither drained or fluctuating lakes were used by males at all in 2007 nor by females in 2009, and in both cases only the open water and land classes were used.

Table 7. Model selection results for the two moose (HRS 2 and 5) for which the drained lake and fluctuating lake variables could be evaluated. Models with higher AIC weights (wi) are better supported by the data.

| Model | Model Structure | AIC weights (wi) | | | | |
|-------|--|------------------|-------|--|--|--|
| Model | Woder Structure | HRS-2 | HRS-5 | | | |
| W1 | Distance to water + Distance to water ² | 0.000 | 0.000 | | | |
| W2 | Diversity | 0.000 | 0.000 | | | |
| W3 | Upright shrub + Open terrain + Woodland | 0.000 | 0.000 | | | |
| W4 | Distance to water + Distance to water ² + Diversity | 0.000 | 0.000 | | | |
| W5 | Diversity + Upright shrub + Open terrain + Woodland | 0.000 | 0.000 | | | |
| W6 | Distance to water + Distance to water ² + Upright shrub + Open terrain + Woodland | 0.000 | 0.000 | | | |
| W7 | Distance to water + Distance to water ² + Diversity + Upright shrub + Open terrain + Woodland | 0.000 | 0.003 | | | |
| W8 | Drained lake + Fluctuating lake | 0.000 | 0.000 | | | |
| W9 | Distance to water + Distance to water ² + Drained lake + Fluctuating lake | 0.000 | 0.000 | | | |
| W10 | Diversity + Drained lake + Fluctuating lake | 0.000 | 0.002 | | | |
| W11 | Upright shrub + Open terrain + woodland + Drained lake + Fluctuating lake | 0.000 | 0.000 | | | |
| W12 | Distance to water + Distance to water ² + Diversity + Drained lake + Fluctuating lake | 0.000 | 0.001 | | | |
| W13 | Diversity + Upright shrub + Open terrain + Woodland + Drained lake + Fluctuating lake | 0.005 | 0.060 | | | |
| W14 | Distance to water + Distance to water ² + Upright shrub + Open terrain + Woodland + Drained lake + Fluctuating lake | 0.045 | 0.002 | | | |
| W15 | Distance to water + Distance to water ² + Diversity + Upright shrub + Open terrain + Woodland + Drained lake + Fluctuating lake | 0.949 | 0.931 | | | |

Table 8. Percentage study area and used points for each of four broad landcover classes in the Old Crow Flats, Yukon.

| Class | Drained Lakes | Fluctuating Lakes | Open Water | Land |
|----------------------|---------------|-------------------|------------|-------|
| Study area | 1.0 | 0.3 | 21.7 | 77.0 |
| All moose, all years | 0.86 | 1.02 | 86.64 | 11.47 |
| Males, all years | 0.10 | 1.83 | 87.22 | 10.86 |
| Females, all years | 1.49 | 0.36 | 86.18 | 11.97 |
| All moose, 2007 | 1.51 | 0.38 | 89.49 | 8.62 |
| All moose, 2008 | 0.76 | 0.97 | 86.48 | 11.80 |
| All moose, 2009 | 0.30 | 2.24 | 82.82 | 14.64 |
| Females, 2007 | 2.38 | 0.60 | 89.29 | 7.74 |
| Females, 2008 | 1.30 | 0.31 | 85.38 | 13.02 |
| Females, 2009 | 0.00 | 0.00 | 82.14 | 17.86 |
| Males, 2007 | 0.00 | 0.00 | 89.85 | 10.15 |
| Males, 2008 | 0.00 | 1.90 | 88.01 | 10.09 |
| Males, 2009 | 0.42 | 3.17 | 83.10 | 13.31 |

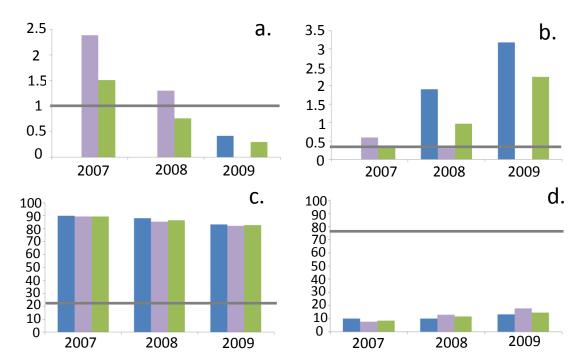


Figure 7. Percentage of used location points for male (blue bars), female (purple bars) and total (green bars) moose in each of four broad landcover classes: a) drained lakes, b) fluctuating lakes, c) open water, and d) land, for each of the three study years (2007 to 2009) in the Old Crow Flats, Yukon. The grey line indicates the proportion of the study area comprised of the landcover class. Bars occurring above this line indicate that use of the landcover class was greater than its availability while bars occurring below this line indicate that use of the landcover class was less than its availability.

Model Validation

Overall, the population-level model performed moderately-well in the k-fold cross validation using the mean frequency values ($r_s = 0.783$, p<0.05; Figure 8a). There was a considerable

level of variability among the five subsets (r_s range: 0.267 to 0.783; Figure 8b). Furthermore, it was difficult to find a break point between bins 4 and 5 using quantiles in ArcGIS 10.0 and these bins were therefore pooled together.

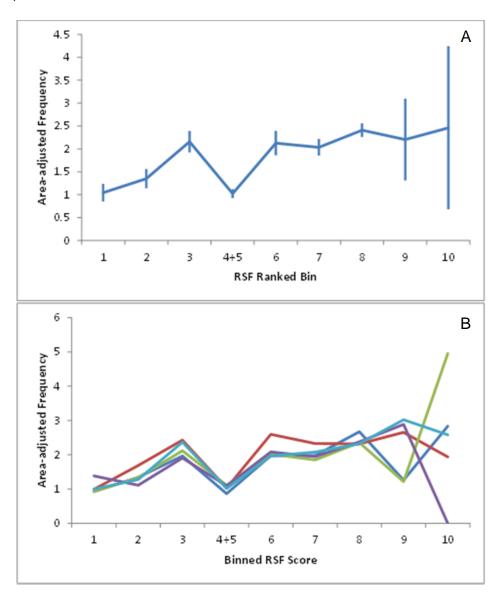


Figure 8. Area-adjusted frequency of binned RSF scores for the k-fold cross validation of the population-level model. a) Mean (±SD) frequency values by binned RSF scores; b) Frequency values for each model subset (n=5; depicted by different colours).

Grouping Moose

A greater amount of variation among individual moose home range models was anticipated than what was observed. One original goal of the study was to explore any observed variation in habitat selection models by grouping moose by sex, geographic locations, or migratory behaviour to determine whether subsets of moose selected habitat similarly based on one or more of these characteristics. However, habitat selection was best explained by Model 7 for most moose (Table 4), suggesting that the majority of moose were selecting similar habitat, regardless of these

characteristics. Because of this similarity in habitat selection, the grouping of moose HRS for further analysis was unnecessary.

The population-level model was applied to all HRS using the buffers around each used GPS location to create the boundary for each HRS (Figure 9). Areas around lakes and rivers showed the highest predicted RSF values within all of the HRS of collared moose within OCF. Extrapolating the model to the entire study area reinforces the importance of waterbodies for moose at this scale of selection (Figure 10).

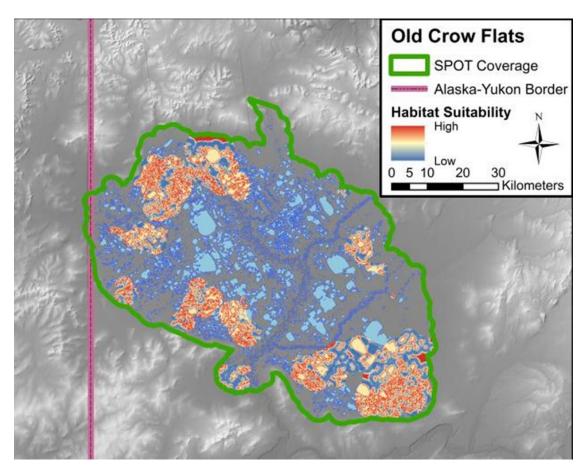


Figure 9 Average relative habitat suitability for moose in summer within their home range sections in Old Crow Flats, Yukon. SPOT coverage refers to study area and represents the extent of the landcover and aquatic features classification. Habitat suitability is displayed as a stretched value between 0 and 1.

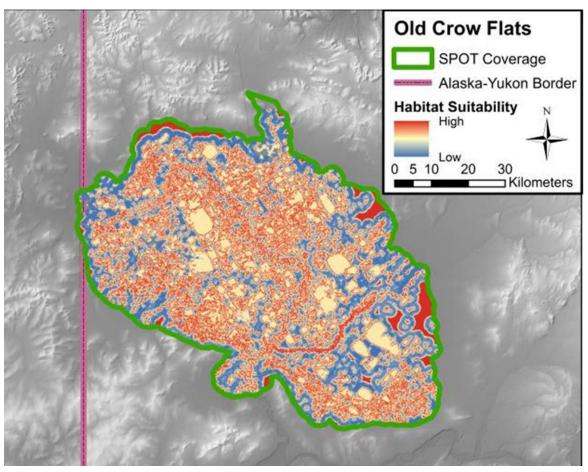


Figure 10 Average relative habitat suitability for moose in summer extrapolated across the entire study area of Old Crow Flats, Yukon. SPOT coverage refers to study area and represents the extent of the landcover and aquatic features classification. Habitat suitability is displayed as a stretched value between 0 and 1. The areas of very high habitat suitability around the north and north-east boundary of the study area are due to a higher abundance of woodland and/or shrubland and a lower abundance of wetlands.

Discussion

Model Application

Summer habitat selection by moose is important to understand because this season is a key time for building fat reserves (Dungan and Wright 2005) and provides important habitats for females with calves (Miquelle et al. 1992). Suitable, available summer habitat should enable moose and their calves to increase their likelihood of surviving the subsequent winter when food supplies are reduced.

Summer habitat is also strongly tied to aquatic resources which are often affected by a changing climate (Vincent 2009; Duguay et al. 2003). As the climate continues to warm in the OCF region, changes to aquatic features such as waterbody type, size, and plant composition are expected to continue (Lantz and Turner 2015). Understanding how the landscape is currently used by moose and the importance of aquatic features can help to predict the effects of landscape changes on moose populations.

Past work has shown that moose habitat selection patterns are complex

and vary by population (Osko et al. 2004; Smits 1991), individuals (Mauer 1998; Poole et al. 2007; Smits 1991), seasons (Courtois et al. 2002; Poole and Stuart-Smith 2006; Smits 1991), and sex (Bowyer et al. 2001; Dussault et al. 2005a; Dussault et al. 2005b). However, the models developed in this study suggest that individual moose in the OCF are largely similar in their habitat selection patterns at the within-home-range spatial scale (3rd-4th order selection; Johnson 1980). This pattern of uniformity observed also implies that there were no subgroups of moose, based on sex, geographic location, or migratory behaviour for example, that select habitat differently than other subgroups.

One moose in the study did not follow the same general pattern as the others. Results indicated that this particular moose selected for the diversity of vegetation types, but not the distance to water or the amount of upright shrubs like the other moose did. The reasons for this difference are largely unknown, but it may reflect subtle differences in the features within this moose's home range section or it may simply reflect the natural variation among individuals.

By quantifying habitat selection, habitat suitability can be classified and mapped across the study area. In general, suitable summer moose habitat must provide adequate forage to support the rearing of young and replenishment of fat reserves, and offer protection from predators and thermal cover. Moose spend a significant part of their day foraging on terrestrial and aquatic vegetation (Franzmann and Schwartz 2007; Milligan 2010). The results of the

habitat selection analysis indicate that for moose, regardless of their sex, the most suitable habitats are those that are closer to water (however, not immediately adjacent), with greater amounts of upright shrubs and a diversity of vegetation types in the nearby vicinity. These findings correspond well with the current understanding of moose summer habitat use from other studies.

Moose typically select their habitat based on the availability of forage, often including areas with an abundance of shrubs including a variety of Salix species, Populus tremuloides, and Betula glandulosa (Dungan and Wright 2005; Van Ballenberghe et al. 1989). Selection for areas of high vegetation diversity has also been reported for moose in Norway during summer (Hjeljord et al. 2006). Moose in that study varied their foraging habits in summer in response to the occurrence of specific forage species, browse height, and variation in plant phenology, likely resulting from changes in light and shade conditions and their effects on forage quality.

Aquatic areas are also important summer habitat, as forage abundance is higher than surrounding habitats, forage quality is higher because of increased sodium concentrations, and the risk of predation may be reduced (Bump et al. 2009; Fraser et al. 1980; Maccracken et al. 1993). In addition to foraging on aquatic vegetation, moose may also be drawn to water during summer to relieve heat stress (Renecker and Hudson 1986), or to escape insects or predators. Although aquatic features on the landscape are important for moose, they may not spend large amounts of time actually

in the water. For example, moose in Isle Royale spent only an hour per day feeding on aquatic plants (Tischler 2004). Thus, one must be careful not to confuse the time spent in an area with its importance to the individual.

A stable isotope analysis of moose summer diet in the OCF (Milligan 2010) showed that moose primarily consumed upland willow shrub, although approximately 7-21% of their diet consisted of aquatic vegetation (Carex spp., Comarum palustre, Equisetum fluviatile, Sparganium sp., S. hyperboreum, Myriophyllum sibiricum, Potamogeton zosterifolium, richardsonii, P. pusillus, P. alpinus, P. praelongus). Our results indicating that moose in the OCF select sites closer to water support previous work showing that aquatic sites are important for moose foraging. However, unlike the spatial variation observed with the consumption of aquatic forage (Milligan 2010) the current study does not suggest any significant spatial variation in selection for aquatic habitats.

The initial purpose of this study was to address local interest and examine the influence of drained and fluctuating lakes in the OCF on the habitat selection of moose. Unfortunately, data were not available to model this relationship for most collared moose because these lake types are relatively uncommon in the OCF compared to other types of land cover. For the two moose where drained and fluctuating lakes were sufficiently abundant in their HRS to include in the models, the results suggest that although they did not have the greatest influence on habitat selection compared to the other

variables, both lake types were selected for, with the strength of this selection differing between home ranges.

The more broad-scale analysis on the relative use of the two lake types indicated that overall, fluctuating lakes were used more often than expected given their abundance on the landscape. When looking at differences in use between the two sexes, females appeared to favor drained lakes while males favored fluctuating lakes. The reason for female preference of drained lakes in unknown, however it may be due to the presence of dead willows in these areas, which may provide cover from predators. Alternatively, males may have less of a concern over predation and use fluctuating lakes to forage on the emergent aquatic vegetation and shrubby riparian areas they provide. Differences in relative use among the three study years suggests that annual variation in climatic conditions (e.g. precipitation, melting, freezing, etc.), predation pressure and/or forage availability may play a role in selection of waterbody type. These results however, are highly generalized and should be interpreted with caution. The phenomenon of lakes draining, or drying, has been noted by residents of Old Crow (Arctic Borderlands Ecological Knowledge Coop 2007). An analysis by Lantz and Turner (2015) shows that catastrophic lake drainage associated with thermokarst processes has the largest impact on lake area in the OCF. This analysis also suggests that an increase in the frequency of catastrophic lake drainage has been caused by increases in regional precipitation and temperature; this

trend is likely to continue. The importance of drained lakes on moose habitat selection, as indicated by the predictive models for HRS2 and HRS5 and by the broad-scale relative use analysis, thus suggests that moose habitat quality may increase over time across the OCF, at least at a fine scale.

Model Limitations and Future Work

All habitat selection models have limitations that may affect their interpretation and application. In the case of this study, there are several such issues that relate to the models developed and the conclusions that can be made.

First, it is important to understand the spatial scale of the analysis. Although moose were collared across the OCF, the scale of the analysis was at the site level (3rd/4th order; Johnson 1980). This scale was selected to identify local features within a moose's selected home range that are driving specific site selection. The factors that influence habitat selection may vary depending on the scale at which the selection is occurring (Dussault et al. 2006; Maier et al. 2005; Mansson et al. 2007). For example, had this study assessed selection at a coarser scale (i.e. 1st/2nd order) it may have identified different factors contributing to moose selection of a specific home range within the OCF, or even the selection of the OCF region within the larger landscape. Thus, the conclusions one makes about habitat use and suitability must be made in consideration of the spatial scale of the analysis.

Second, because the models explained only a small portion of the variation in the data (generally <10%), there are likely other important factors affecting habitat selection that were not captured in this study. This occurred despite best efforts to include habitat descriptors that were hypothesized to be important for moose based on previous studies and expert opinion. Additional habitat information could increase the power and predictive ability of the models created for the spatial scale of this study. For example, moose in northern forests are known to use early-successional habitats due to their increased browse production (Maier et al. 2005; Nelson et al. 2008). However, as vegetation succession proceeds, the area will eventually begin to decline in forage quality and will no longer attracts moose to the same extent (Maier et al. 2005). Thus, information on the age classes of the various habitat types available to moose may be useful. Other potentially useful habitat data to include are the locations of mineral licks which are known to influence the spatio-temporal structure of moose populations (Panichev et al. 2002). Moose typically visit mineral licks between dusk and dawn (Tankersley and Gasaway 1983) throughout the year, although spring and early summer are considered the key periods of use due to nutritional requirements (Ayotte et al. 2006; Rea et al. 2004).

Third, while collar locations recorded during long-distance movements were excluded from the analysis (hence multiple HRSs for a single moose), it is possible that the inclusion of points during short travel distances not only increased variation in the data, but were also not "selected" in a sense that could be described by the covariates used in the models. Further, random individual variation in selection among moose may have affected smaller-scale habitat selection moreso than selection at larger spatial scales.

Fourth, although the final model performed moderately-well in the kfolds cross validation, there was high variability in the performance of the cross-validated models among the different validation subsets. These results suggest that although some of the important features for moose at this scale of selection may have been captured in the model, there are other important variables that were not assessed in the current study. For example, the effect of predator presence was not included as the data to assess this was not available for the study area. Furthermore, other moose on the landscape may affect habitat availability via direct or indirect competition for resources; however this was unknown and not accounted for in the models.

Fifth, moose habitat selection in the current study was assumed to be constant during the summer season. Moose are known to change their selection criteria during summer as a result of plant phenology (e.g., based on changes in foraging conditions and quality; Hjeljord et al. 2006). Similarly, an analysis of the dietary habits of moose in the OCF indicated that moose alter their foraging patterns (i.e., the relative proportions of terrestrial versus aquatic forage in the diet) as the seasons progress from winter to spring (Milligan 2010).

Future habitat selection modeling and dietary analysis could consider intraseasonal variation in site and forage selection as a means to better understand the effects of plant phenology on moose behaviour during summer.

Sixth, collar location data in the current study was collected every 4 or 5 hours, depending on the collar. While this is a common schedule for collared ungulate studies, it may be informative to collect location data on a shorter time interval (e.g., every 30 minutes) to better understand how moose use aquatic features on the landscape. It is well-known that moose are drawn to lakes to forage on aquatic vegetation, but they may only be in the lake for short periods of time (Tischler 2004). Shorter intervals between relocations may allow for a greater understanding of how moose use lakes for foraging.

Lastly, it is common for bias in the description of available habitat to exist in resource selection studies, with the degree of this bias dependent on the number of points used to describe resource availability. If significant, this bias can create a degree of error in the variable coefficient values. In this study, five random points were selected within each location buffer to describe the available resources. While a ratio of 5:1 (or lower) is commonly used in other similar studies (e.g. Florkiewicz et al. 2007, Carroll et al. 2006), a greater number of random points may lower any existing bias. To determine the extent of this error in the current study, the analysis could be re-run using a larger number of available points and the change in coefficient values could be assessed.

Overall, the habitat models developed in this study described a portion of the summer habitat selection patterns of adult moose in the OCF. The models were relatively uniform across moose of both sexes and across the full spatial range of the OCF. As anticipated, both terrestrial and aquatic landscape features were selected by moose at the scale of analysis. As such, the models may be used to generally predict the relative probability of occurrence of moose within the study area. Caution must be exercised however, as the models explained only a portion of the variation associated with moose habitat selection; as previously stated,

there are other features driving selection that remain unidentified.

As with all predictive models, the models developed in this study should be revised and re-validated accordingly as new data becomes available. A nice complement to this study would be an analysis of summer habitat selection at a larger spatial scale, such as the selection of home range (Johnson 1980). The combination of models for small- and large-scale habitat selection would provide a more complete assessment of the factors governing habitat use by moose in the OCF.

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Appendix A Results of top summer habitat selection models for each moose Home Range Section (HRS) analysed. Top models were selected from a larger set of candidate models using AIC values. The model used to map habitat suitability for each individual HRS is indicated in bold. *Indicates a model including waterbody condition variables.

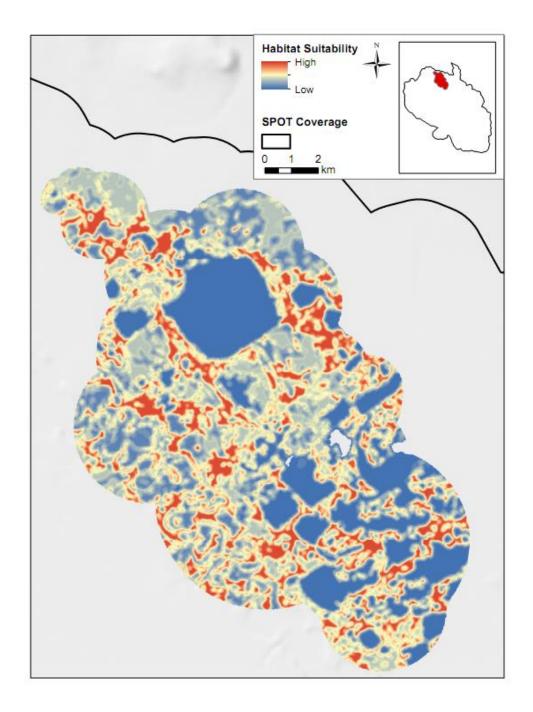
| HRS | Model | Variable | Coefficient | Standard | z-value | p | Null | Residual |
|--|-------|--------------------------------|-------------|----------|---------|-------------|----------|----------|
| | _ | | estimate | error | | value | deviance | deviance |
| 1 | 5 | Diversity | 0.169 | 0.056 | 3.005 | 0.003 | 3246 | 3163 |
| | | Upright shrub | 0.547 | 0.073 | 7.486 | <0.00 | | |
| | | | | | | 01 | | |
| | | Open terrain | 0.195 | 0.074 | 2.639 | 0.008 | | |
| | | Woodland | 0.045 | 0.099 | 0.452 | 0.651 | | |
| | _ | | 2 12 - | | 4.050 | 2 2 2 2 | 22.12 | 2452 |
| 1 | 7 | Distance to Water | -0.425 | 0.257 | -1.656 | 0.098 | 3246 | 3159 |
| | | Distance to water ² | 0.053 | 0.069 | 0.763 | 0.446 | | |
| | | Diversity | 0.137 | 0.059 | 2.329 | 0.020 | | |
| | | Upright shrub | 0.619 | 0.863 | 7.174 | <0.00 01 | | |
| | | Open terrain | 0.269 | 0.086 | 3.120 | 0.002 | | |
| | | Woodland | 0.130 | 0.111 | 1.166 | 0.244 | | |
| | | | | | | | | |
| 2 | 7 | Distance to Water | -0.950 | 0.270 | -3.525 | 0.000 4 | 2354 | 2291 |
| | | Distance to water ² | 0.2773 | 0.116 | 2.393 | 0.017 | | |
| | | Diversity | 0.166 | 0.055 | 3.024 | 0.003 | | |
| | | Upright shrub | 0.461 | 0.101 | 40.580 | <0.00 01 | | |
| | | Open terrain | -0.003 | 0.089 | -0.034 | 0.973 | | |
| | | Woodland | 0.209 | 0.091 | 2.298 | 0.021 6 | | |
| | | | | | | | | |
| 2 | 15* | Distance to Water | -1.001 | 0.272 | -3.676 | 0.000 2 | 2354 | 2268 |
| | | Distance to water ² | 0.296 | 0.116 | 2.554 | 0.011 | | |
| | | Diversity | 0.158 | 0.056 | 2.840 | 0.005 | | |
| | | Upright shrub | 0.469 | 0.101 | 4.621 | <0.00 01 | | |
| | | Open terrain | -0.031 | 0.090 | -3.50 | 0.726 | | |
| | | Woodland | 0.222 | 0.091 | 2.434 | 0.015 | | |
| | | Dried lake | 0.140 | 0.042 | 3.369 | 0.000 | | |
| | | Fluctuating | 0.388 | 0.097 | 3.995 | <0.00 | 1 | |
| | | lake | 3.000 | 3.001 | 3.555 | 01 | | |

| 3 | 5 | Diversity | 0.244 | 0.065 | 3.753 | 0.0002 | 3128 | 3071 |
|---|-----|--------------------------------|--------|--------|--------|---------|------|------|
| | - | Upright shrub | 0.448 | 0.100 | 4.474 | <0.0001 | 1 | |
| | | Open terrain | -0.163 | 0.103 | -1.583 | 0.113 | | |
| | | Woodland | 0.282 | 0.091 | 3.088 | 0.002 | | |
| | | | 00 | 0.00 | 0.000 | 0.100 | | |
| 3 | 7 | Distance to Water | -0.366 | 0.175 | -2.087 | 0.037 | 3128 | 3066 |
| | | Distance to water ² | 0.043 | 0.036 | 1.208 | 0.227 | | |
| | | Diversity | 0.211 | 0.0663 | 3.178 | 0.002 | | |
| | | Upright shrub | 0.556 | 0.113 | 4.941 | <0.0001 | | |
| | | Open terrain | -0.070 | 0.111 | -0.625 | 0.532 | | |
| | | Woodland | 0.366 | 0.100 | 3.662 | 0.0003 | | |
| | | | | | | | | |
| 4 | 7 | Distance to Water | -1.706 | 0.338 | -5.040 | <0.0001 | 1953 | 1838 |
| | | Distance to water ² | 0.685 | 0.209 | 3.278 | 0.001 | | |
| | | Diversity | 0.300 | 0.074 | 4.034 | <0.0001 | | |
| | | Upright shrub | 0.877 | 0.117 | 7.510 | <0.0001 | | |
| | | Open terrain | 0.414 | 0.122 | 3.393 | 0.0006 | | |
| | | Woodland | 0.530 | 0.128 | 4.137 | <0.0001 | | |
| | | | | | | | | |
| 5 | 7 | Distance to Water | 0.693 | 0.251 | -2.756 | 0.006 | 3163 | 3116 |
| | | Distance to water ² | 0.198 | 0.101 | 1.970 | 0.049 | | |
| | | Diversity | 0.216 | 0.050 | 4.322 | <0.0001 | | |
| | | Upright shrub | 0.353 | 0.110 | 3.223 | 0.001 | | |
| | | Open terrain | 0.024 | 0.088 | 0.270 | 0.787 | | |
| | | Woodland | 0.207 | 0.082 | 2.518 | 0.012 | | |
| | | | | | | | | |
| 5 | 15* | Distance to Water | -0.763 | 0.253 | -3.021 | 0.003 | 3163 | 3101 |
| | | Distance to water ² | 0.223 | 0.100 | 2.216 | 0.027 | | |
| | | Diversity | 0.185 | 0.051 | 3.645 | 0.0003 | | |
| | | Upright shrub | 0.362 | 0.110 | 3.276 | 0.001 | | |
| | | Open terrain | 0.035 | 0.0887 | 0.398 | 0.691 | | |
| | | Woodland | 0.214 | 0.082 | 2.605 | 0.009 | | |
| | | Dried lake | 0.117 | 0.030 | 3.914 | <0.0001 | | |
| | | Fluctuating lake | 0.030 | 0.103 | 0.295 | 0.768 | | |
| | | | | | | | | |
| 6 | 7 | Distance to Water | -0.868 | 0.435 | -1.994 | 0.050 | 516 | 500 |
| | | Distance to water ² | 0.463 | 0.403 | 1.150 | 0.250 | | |
| | | Diversity | 0.295 | 0.136 | 2.168 | 0.030 | | |
| | | Upright shrub | 0.291 | 0.158 | 1.847 | 0.065 | | |
| | | Open terrain | -0.252 | 0.252 | -1.000 | 0.318 | | |
| | | Woodland | -0.088 | 0.220 | -0.402 | 0.688 | | |
| | | | | | | | | |
| 6 | 5 | Diversity | 0.383 | 0.129 | 2.977 | 0.003 | 516 | 504 |
| | | Upright shrub | 0.181 | 0.142 | 1.268 | 0.205 | | |
| | | Open terrain | -0.355 | 0.239 | -1.483 | 0.138 | | |
| | | Woodland | -0.218 | 0.209 | -1.043 | 0.297 | | |
| | | | | | | | | |
| 6 | 2 | Diversity | 0.246 | 0.117 | 2.109 | 0.035 | 516 | 512 |
| | | | | | | | | |
| 7 | 4 | Distance to Water | -1.467 | 0.272 | -5.398 | <0.0001 | 1283 | 1189 |
| | | Distance to water ² | 1.096 | 0.205 | 5.350 | <0.0001 | | |
| | | Diversity | 0.550 | 0.082 | 6.752 | <0.0001 | | |

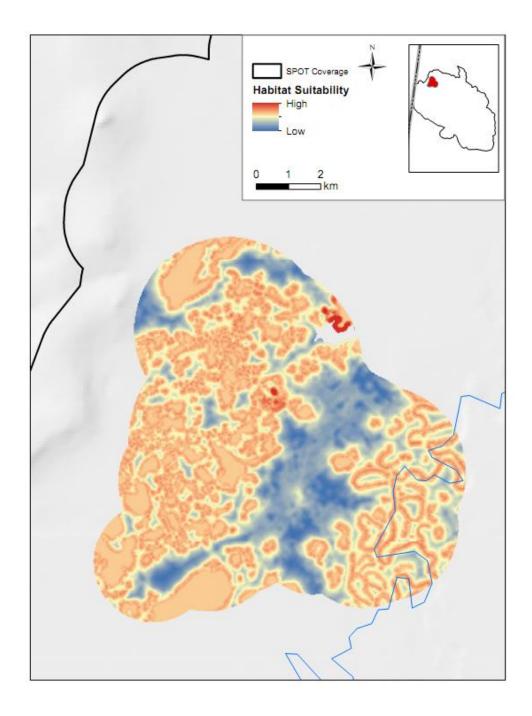
| 7 | 7 | Distance to Water | -2.000 | 0.380 | -5.268 | <0.0001 | 1283 | 1184 |
|----|---|--------------------------------|-----------------|--------|-----------------|-----------------|------|------|
| | | Distance to water ² | 1.404 | 0.257 | 5.461 | <0.0001 | | |
| | | Diversity | 0.484 | 0.099 | 4.882 | <0.0001 | | |
| | | Upright shrub | 0.274 | 0.121 | 2.259 | 0.024 | | |
| | | Open terrain | 0.156 | 0.179 | 0.871 | 0.384 | | |
| | | Woodland | 0.247 | 0.162 | 1.527 | 0.127 | | |
| | | 11000 | 3.2 | 352 | 11021 | U.I. | | |
| 8 | 7 | Distance to Water | -1.606 | 0.305 | -5.258 | <0.0001 | 1874 | 1719 |
| | - | Distance to water ² | 0.542 | 0.164 | 3.300 | 0.001 | 1011 | 1110 |
| | | Diversity | 0.452 | 0.072 | 6.265 | <0.0001 | | |
| | | Upright shrub | 0.656 | 0.111 | 5.912 | <0.0001 | | |
| | | Open terrain | 0.341 | 0.111 | 3.075 | 0.002 | | |
| | | Woodland | 0.156 | 0.129 | 1.213 | 0.225 | | |
| | | Woodiana | 0.100 | 0.123 | 1.210 | U.ZZU | | |
| 9 | 2 | Diversity | 0.1821 | 0.1330 | 1.369 | 0.171 | 373 | 371 |
| | | | | | | _ | | |
| 9 | 5 | Diversity | 0.291 | 0.155 | 1.880 | 0.060 | 373 | 365 |
| | | Upright shrub | -0.023 | 0.190 | -0.120 | 0.904 | | |
| | | Open terrain | -0.534 | 0.337 | -1.582 | 0.114 | | |
| | | Woodland | -0.270 | 0.174 | -1.548 | 0.122 | | |
| | | | | | | | | |
| 10 | 6 | Distance to Water | -1.9450 | 0.573 | -3.394 | 0.001 | 222 | 197 |
| 10 | | Distance to water ² | 0.342 | 0.170 | 2.009 | 0.045 | LLL | 131 |
| | | Upright shrub | 0.939 | 0.378 | 2.481 | 0.013 | | |
| | | Open terrain | -0.288 | 0.355 | -0.812 | 0.417 | | |
| | | Woodland | 0.549 | 0.301 | 1.825 | 0.068 | | |
| | | VVOCalaria | 0.043 | 0.001 | 1.020 | 0.000 | | |
| 10 | 7 | Distance to Water | -1.787 | 0.597 | -2.993 | 0.003 | 222 | 196 |
| | | Distance to water ² | 0.314 | 0.176 | 1.786 | 0.074 | | |
| | | Diversity | 0.273 | 0.250 | 1.093 | 0.274 | | |
| | | Upright shrub | 0.983 | 0.398 | 2.472 | 0.013 | | |
| | | Open terrain | -0.442 | 0.399 | -1.108 | 0.268 | | |
| | | Woodland | 0.597 | 0.316 | 1.886 | 0.059 | | |
| | | | 0.001 | 0.0.0 | 1.000 | 0.000 | | |
| 11 | 7 | Distance to Water | -1.174 | 0.391 | -3.001 | 0.003 | 891 | 843 |
| | | Distance to water ² | 0.277 | 0.271 | 1.022 | 0.307 | | |
| | | Diversity | 0.103 | 0.087 | 1.188 | 0.235 | | |
| | | Upright shrub | 0.653 | 0.152 | 4.283 | <0.0001 | | |
| | | Open terrain | 0.048 | 0.126 | 0.376 | 0.707 | | |
| | | Woodland | 0.101 | 0.152 | 0.666 | 0.506 | | |
| | | | 2 | | | 2.2.3.4 | | |
| 12 | 7 | Distance to Water | -0.970 | 0.162 | -5.990 | <0.0001 | 3335 | 3134 |
| | | Distance to water ² | 0.225 | 0.058 | 3.865 | 0.0001 | | |
| | | Diversity | 0.274 | 0.042 | 6.570 | <0.0001 | | |
| | + | Upright shrub | 0.691 | 0.077 | 8.954 | <0.0001 | | |
| | | - F G | | 0.066 | 3.791 | 0.0002 | | |
| | | Open terrain | 0.249 | | | | 1 | _ |
| | | Open terrain Woodland | 0.249 | | _ | | | |
| | | Open terrain Woodland | 0.249 | 0.068 | 2.580 | 0.01 | | |
| 13 | 7 | Woodland | 0.175 | 0.068 | 2.580 | 0.01 | 3003 | 2822 |
| 13 | 7 | Woodland Distance to Water | 0.175 -1.550 | 0.068 | 2.580 -5.071 | 0.01 <0.0001 | 3003 | 2822 |
| 13 | 7 | Woodland | 0.175 | 0.068 | 2.580 | 0.01 | 3003 | 2822 |

| | | Open terrain | 0.379 | 0.091 | 4.185 | <0.0001 | | |
|----|---|--------------------------------|--------|-------|--------|---------|------|------|
| | | Woodland | 0.139 | 0.138 | 1.005 | 0.315 | | |
| | | | | | | | | |
| 14 | 7 | Distance to Water | -1.469 | 0.249 | -5.900 | <0.0001 | 3218 | 2982 |
| | | Distance to water ² | -0.417 | 0.403 | -1.033 | 0.301 | | |
| | | Diversity | 0.292 | 0.046 | 6.413 | <0.0001 | | |
| | | Upright shrub | 0.668 | 0.097 | 6.921 | <0.001 | | |
| | | Open terrain | 0.121 | 0.080 | 1.505 | 0.132 | | |
| | | Woodland | 0.063 | 0.099 | 0.634 | 0.526 | | |
| | | | | | | | | |
| 16 | 7 | Distance to Water | -0.569 | 0.154 | -3.683 | 0.0002 | 2199 | 2114 |
| | | Distance to water ² | 0.079 | 0.022 | 3.635 | 0.0003 | | |
| | | Diversity | 0.225 | 0.072 | 3.124 | 0.002 | | |
| | | Upright shrub | 0.814 | 0.107 | 7.634 | <0.0001 | | |
| | | Open terrain | 0.316 | 0.095 | 3.336 | 0.001 | | |
| | | Woodland | 0.316 | 0.137 | 2.309 | 0.021 | | |
| | | | | | | | | |
| 17 | 7 | Distance to Water | -0.980 | 0.393 | -2.494 | 0.013 | 1183 | 1151 |
| | | Distance to water ² | 0.227 | 0.130 | 1.743 | 0.081 | | |
| | | Diversity | 0.282 | 0.083 | 3.390 | 0.0007 | | |
| | | Upright shrub | 0.478 | 0.150 | 3.183 | 0.002 | | |
| | | Open terrain | 0.311 | 0.145 | 2.152 | 0.031 | | |
| | | Woodland | 0.117 | 0.186 | 0.626 | 0.531 | | |
| | | | | | | | | |
| 17 | 2 | Diversity | 0.331 | 0.074 | 4.453 | <0.0001 | 1183 | 1162 |

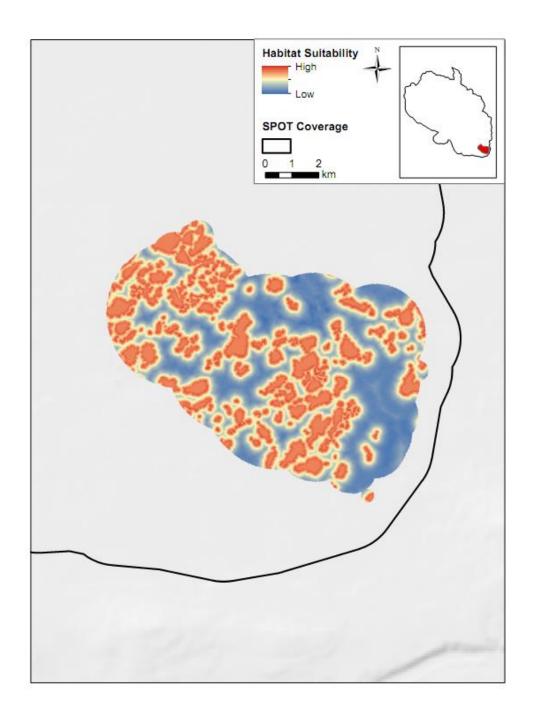
Appendix B Relative suitability of habitat for moose in summer in each individual home range section in Old Crow Flats, Yukon. Variables that contribute to each home range-specific resource selection model are summarized in Appendix A and indicated as "Top Model". SPOT coverage refers to study area and represents the extent of the landcover and aquatic features classification.



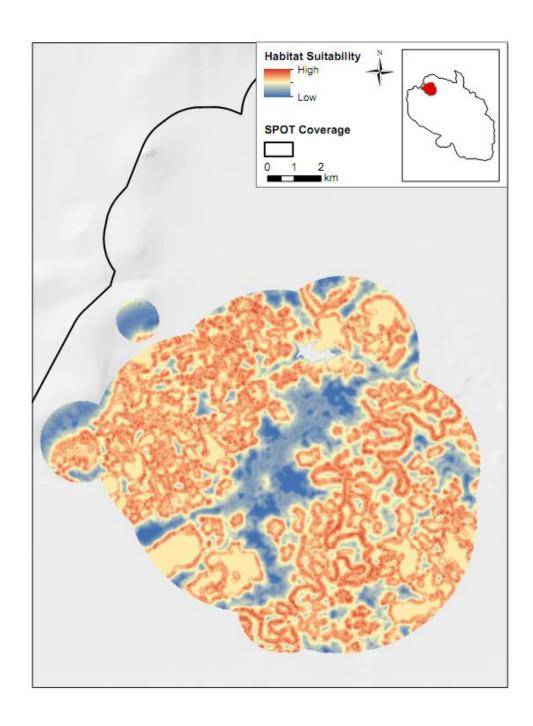
B 1 Relative suitability of habitat for moose in summer in Home Range Section 1.



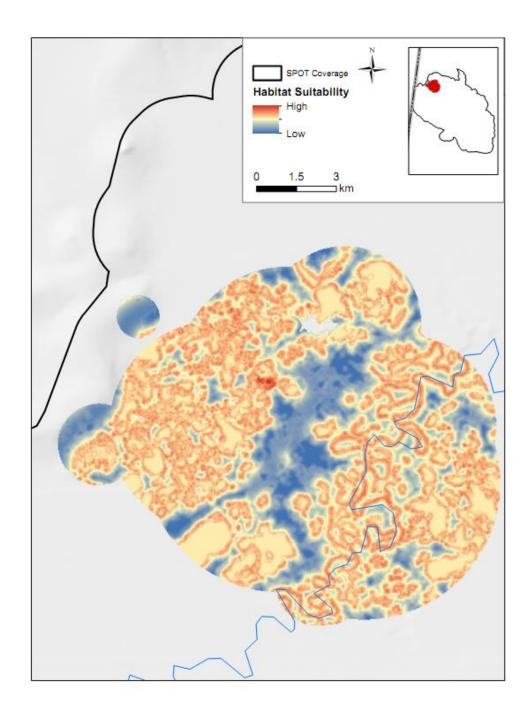
B 3 Relative suitability of habitat for moose in summer in Home Range when lake condition variables are considered Section 2.



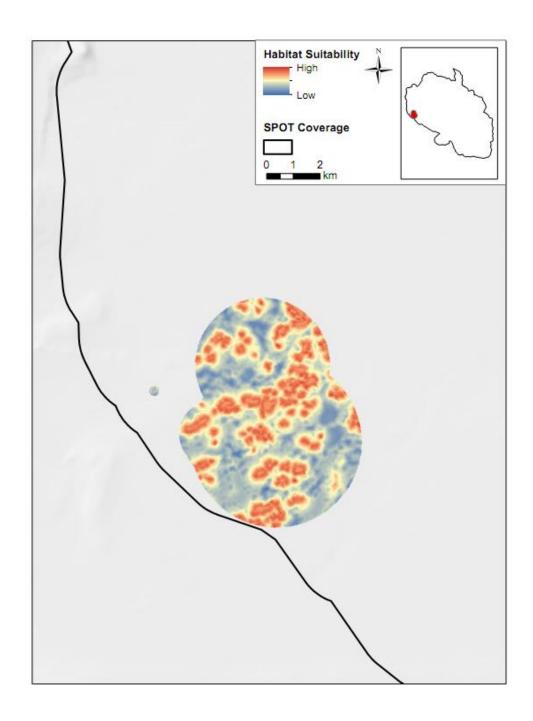
B 5 Relative suitability of habitat for moose in summer in Home Range Section 4.



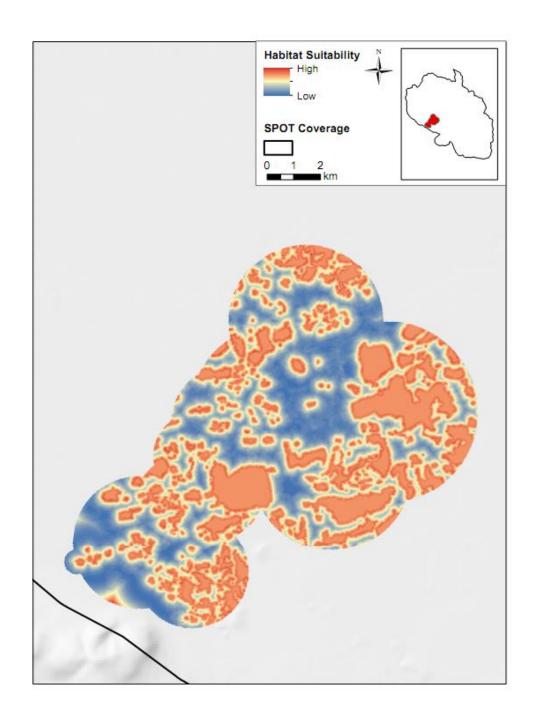
B 6 Relative suitability of habitat for moose in summer in Home Range Section 5.



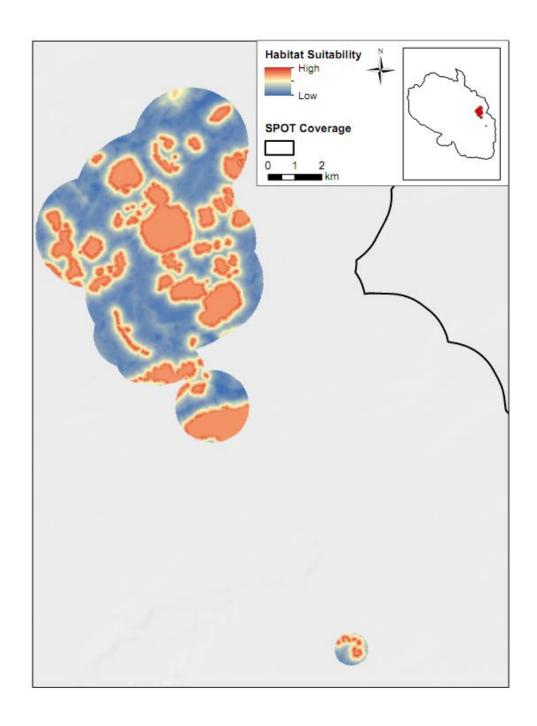
B 7 Relative suitability of habitat for moose in summer in Home Range when lake condition variables are considered Section 5.



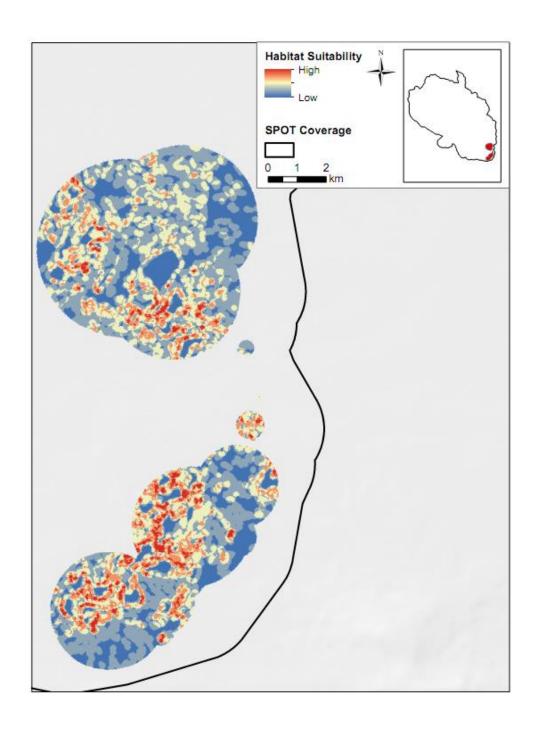
B 8 Relative suitability of habitat for moose in summer in Home Range Section 6.



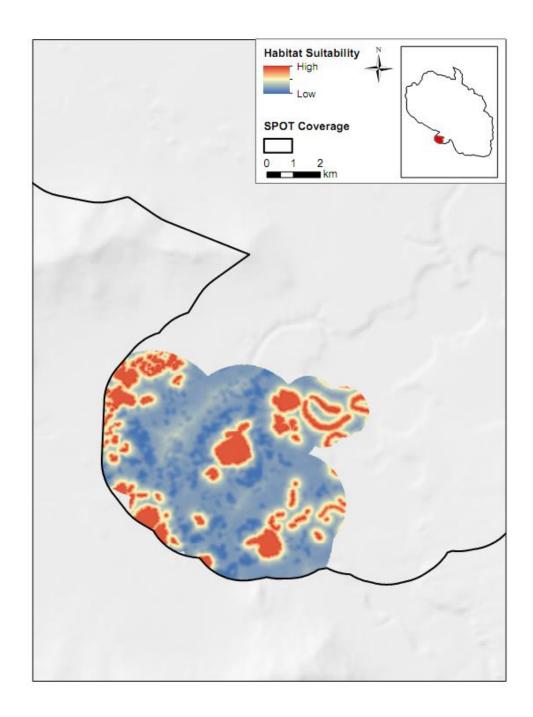
B 9 Relative suitability of habitat for moose in summer in Home Range Section 7.



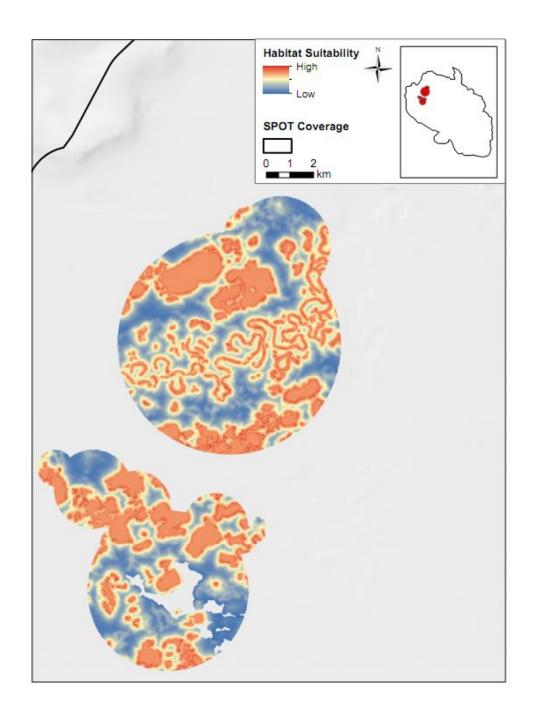
B 10 Relative suitability of habitat for moose in summer in Home Range Section 8.



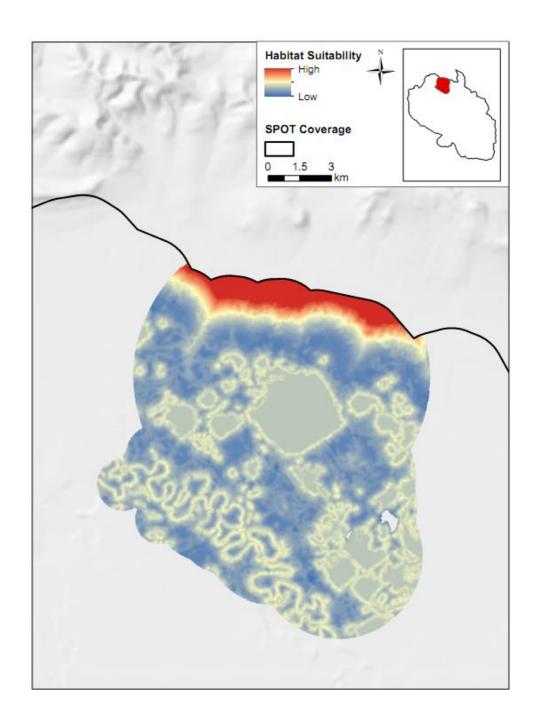
B.11 Relative suitability of habitat for moose in summer in Home Range Section 9.



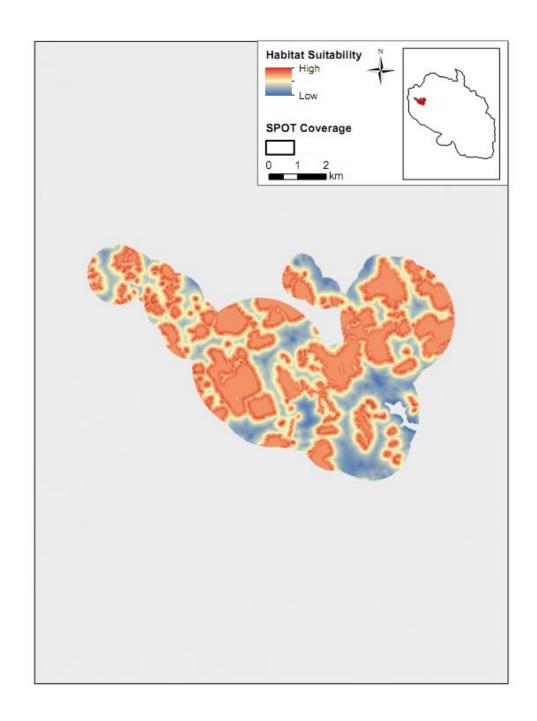
B 12 Relative suitability of habitat for moose in summer in Home Range Section 10.



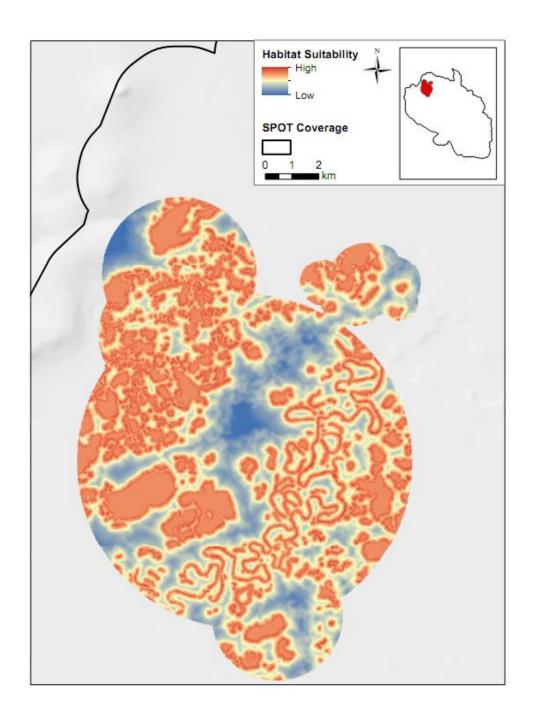
B 13 Relative suitability of habitat for moose in summer in Home Range Section 11.



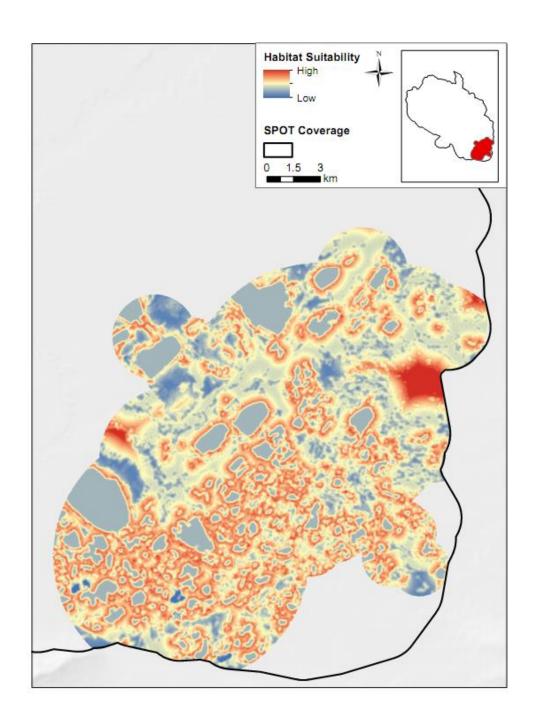
B 14 Relative suitability of habitat for moose in summer in Home Range Section 12.



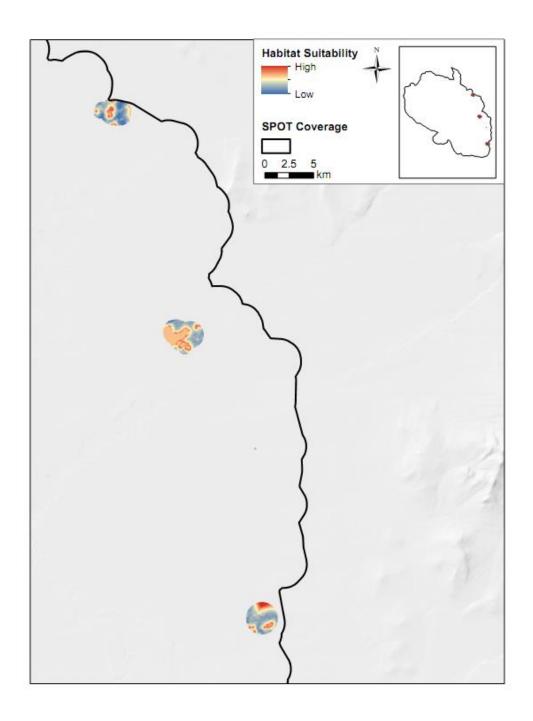
B 15 Relative suitability of habitat for moose in summer in Home Range Section 13.



B 16 Relative suitability of habitat for moose in summer in Home Range Section 14.



B 17 Relative suitability of habitat for moose in summer in Home Range Section 15.



B 18 Relative suitability of habitat for moose in summer in Home Range Section 17.