THE EFFECTS OF SEX, TERRAIN, WILDFIRE, WINTER SEVERITY, AND MATERNAL STATUS ON HABITAT SELECTION BY MOOSE IN NORTH-CENTRAL ALASKA

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ABSTRACT: Habitat selection is a central component of the ecology of individual animals as it affects body condition, survivorship, and reproductive output. We instrumented male and female moose (*Alces alces*) in north-central Alaska with GPS radio-collars to assess factors we hypothesized were important to their habitat selection. Using synoptic modeling techniques, we found that models with more covariates were better predictors of moose habitat selection than more simplistic models. As expected, moose selected for habitats with high canopy cover and/or that typically have abundant forage such as 11-30 year old burned areas. However, we detected differences in habitat selection between sexes, seasons (i.e., winter versus summer), during winters of varying severity, and females with differing maternal status. During winter males moved to lower elevations areas, presumably to avoid greater snow depths, whereas females remained at relatively similar elevations. Females selected burned habitat and areas that received higher amounts of solar radiation. We found that all moose selected for lower elevation habitats closer to rivers during moderate and severe winters, but elevation was not a strong influence during mild winters. We found that females with calves avoided riparian habitats and selected areas with more forested habitat than females without calves during both summer and winter. This suggests a trade-off between maximizing forage intake and reducing predation risk for their offspring. Our and similar data are useful to improve moose management strategies and provide a benchmark against which the impacts of climate change and industrial development are assessed in this rapidly-changing region.

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An animal's use of the landscape affects its body condition, reproductive output, survivorship, and fitness (Gaillard et al. 2010). Thus, studies of habitat selection are also informative to understanding the ecology of vagile species. Although habitat selection by moose (*Alces alces*) has been well documented in North American populations (see Peek 1997), there is a paucity of habitat selection studies in northern Alaska. Patterns of selection by moose differ among and within populations, and between sexes and seasons. Alaskan moose are sexually dimorphic in body size, and sexual segregation is well documented (Miquelle et al. 1992, Bowyer et al. 2001, Oehlers et al. 2011). Barboza and Bowyer (2000) suggested that sex-related differences in habitat selection patterns can be explained by differences in body size and annual changes in the physiology and morphology between sexes. Large males are able to consume large quantities of low-quality forage, whereas smaller-bodied females are better adapted for smaller quantities of high-quality forage. Risk of predation is also thought to play a major role in the selection of habitats by moose, particularly females with calves (Dussault et al. 2005, Poole et al. 2007, Oehlers et al. 2011). Moose reduce risk of predation by avoiding travel routes used by predators (Kunkel and Pletscher 1999, Dussault et al. 2005) and selecting habitats that provide greater concealment (Oehlers et al. 2011). Terrain features and snow conditions also influence patterns of distribution and selection by moose (Poole and Stuart-Smith 2006). Within interior mountain areas, moose tend to descend to lower elevation valley bottoms during winter (Poole and Stuart-Smith 2006). Thus, differences in habitat selection patterns among populations of moose are dependent on local conditions with respect to forage, predators, and weather.

Climate change is predicted to profoundly affect land mammals in the Arctic (Lawler et al. 2009, Marcot et al. 2015). Wildfire is already common in the region (Joly et al. 2009) and is predicted to increase under warming scenarios (Kasischke and Turetsky 2006, Johnstone et al. 2010, Joly et al. 2012). Early seral stage shrub communities, which follow wildfires, provide abundant high quality forage for moose (Schwartz and Franzmann 1989). Moreover, moose populations have increased where these early seral habitats have expanded due to wildfire (Spencer and Hakala 1964, Schwartz and Franzmann 1989). Increased shrub abundance has been documented around the Arctic and is thought to be linked to warming (Tape et al. 2006). Thus, climate change may produce more moose habitat and more moose in this region if patterns of selection for early seral stage and shrubby habitats by moose are similar to other areas of the boreal forest (Joly et al. 2012). Understanding current patterns of habitat selection will aid in assessing the effects of climate change into the future.

We analyzed habitat selection by moose on the southern flanks of the Brooks Range and the adjacent lowlands in north-central Alaska (Fig. 1), near the northern extent of moose range in this region. Our goal was to provide information about habitat selection patterns in Alaska's arctic interior to improve moose management. We focused on selection within the home range across individuals during winter and summer seasons using variables we believed important to moose. We assessed whether patterns of habitat selection were driven primarily by spatial factors related to abundance of adequate forage, predator avoidance, or physiography. We hypothesized that habitat selection would be driven by a complex mix of factors, highlighting the trade-offs among access to forage, energy expenditure, and exposure to predation pressure. Further, we hypothesized that maternal status and winter severity would influence patterns of habitat selection. We expected females with calves to select more forested areas further from rivers than females without calves, presumably to reduce predation risk, and that moose would select areas lower in elevation during more severe winters.

METHODS

Study area

This study took place in the upper reaches of the Koyukuk River in north-central Alaska (Fig. 1). The area supported a low density (~ 0.1 moose/km^2) moose population (Lawler et al. 2006), as well as the full complement of naturally occurring species including caribou (*Rangifer tarandus*), Dall's sheep (*Ovis dalli*), wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and black bears (*U. americanus*). The upper Koyukuk River drainage had a strong continental climate with short, hot summers and long, cold winters. Temperatures dropped below – 45 °C and snow persisted on the ground from October until May (Western Regional Climate Center, www.wrcc.dri.edu/).

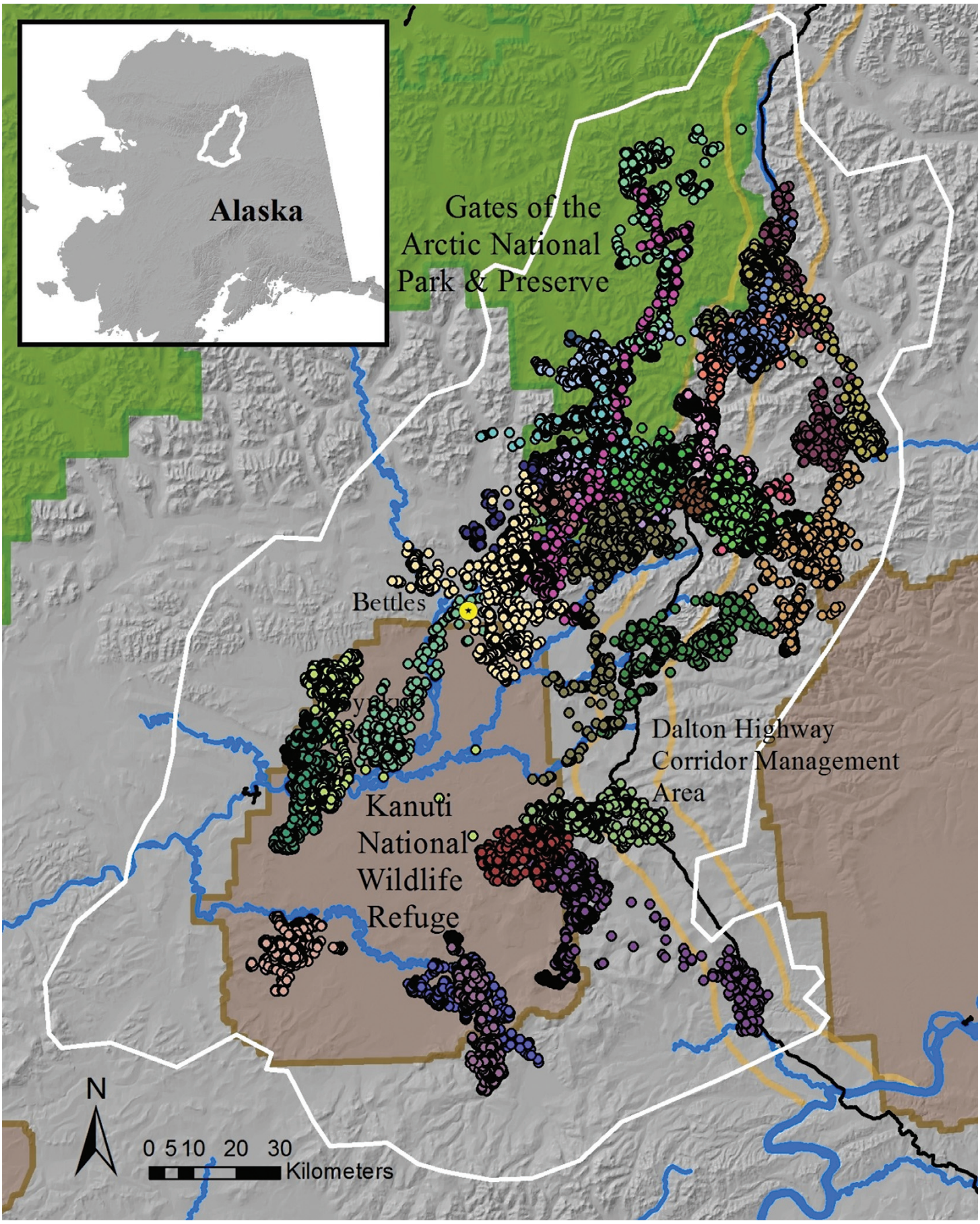

Fig. 1. Moose habitat selection and use study area (white polygon) in north-central Alaska, 2008–2013. GPS locations (dots) of individual moose are color-coded.

Snow pack was typically >60 cm most winters and often >90 cm. Summers were brief but temperatures can exceed 30 °C. Large wildfires were common during warm dry summers, particularly south of the Brooks Range which consisted of boreal forest vegetation dominated by fire-prone communities such as black spruce (*Picea mariana*) forests.

The northern half of the study area consisted of the central Brooks Range - rugged mountains that reach up to 2000 m in elevation that contain narrowly-confined glacial river valleys, and where wildfire is much less common. The valleys supported spruce and birch (*Betula papyrifera*) forests, tussock tundra, shrub lands (*Alnus* spp., *Salix* spp.), and muskeg. Tall and low shrub communities occurred on hillsides, but eventually gave way to alpine vegetation. This area included the southeastern portion of Gates of the Arctic National Park and Preserve (GAAR) and lands managed by the Bureau of Land Management (BLM) and the state of Alaska.

The southern portion of the study area was much less rugged and lower in elevation; typically about 300 m above sea level with hills generally lower than 500 m. It had more wetland habitat, was extensively forested, and wildfires were prevalent. The southern portion of the study area primarily contained lands managed by the Kanuti National Wildlife Refuge (KNWR), the state of Alaska, and the BLM. The town of Bettles, Alaska was in the middle of the study area.

Moose capture, GPS data, maternal status, winter severity

We captured adult male and female moose between March 2008 and April 2011 via aerial darting. Moose were fitted with GPS radio-collars (Telonics TGW-4780) that also had a very high frequency (VHF) radio beacon (Joly et al. 2015a); collars were removed when the project ended in April 2013. Collars collected 3 locations/day except those deployed in March 2008. For our analyses, all location datasets began on 15 May, and we excluded all individual-years that were sampled <330 days.

Maternal status, as indicated by the presence or absence of a calf, was determined by tracking collared females in small, fixed-wing aircraft (e.g., Piper PA-18 Supercub). We attempted to locate all collared females just after calving (late May–early June), in the fall (September–October), and during the following spring (March–April) to visually determine if the female was accompanied by a calf. If we could not make this determination, the individual was excluded from analyses related to maternal status.

We classified each winter as mild, moderate, or severe based on the total number of days with snow and snow depth as recorded in Bettles, Alaska (Joly et al. 2015a). The 3 classifications were: 1) mild winters had <135 days with ≥30 cm snow or <7 days with ≥60 cm snow, 2) moderate winters had >170 days with ≥30 cm snow, >50 days with ≥60 cm, or <14 days with ≥90 cm snow, and 3) severe winters had >170 days with ≥30 cm snow, >100 days with ≥60 cm, or >30 days with ≥90 cm snow. We used these non-continuous categories to highlight that the classifications were distinctive – all winters fell into a single category. Two winters (2009–10, 2012–13) were categorized as mild, 3 (2007–08, 2010–11, and 2011–12) as moderate, and 1 (2008–09) as severe. We defined biological seasons as summer (1 July–24 August) and winter (16 December–14 May) based on regional weather patterns.

Study design

Scale is critical to understanding ecological processes (Wiens 1989, Wheatley and Johnson 2009, DeCesare et al. 2012). Habitat preferences modify with changes in the relative amount of available habitat (Osko et al. 2004, Herfindal et al. 2009). Due to physiographic differences between the northern and southern portions of our study area, we estimated seasonal habitat selection by moose at the home range scale (3rd order; Johnson 1980) using the synoptic model of space use (Horne et al. 2008, Slaght et al. 2013). This model uses a weighted distribution to simultaneously model an individual's space use and habitat selection (Johnson et al. 2008) within its home range, and is capable of estimating home range and resource selection simultaneously. Thus, the probability of use at location x and time t was modeled using:

$$f_u(x,t) = \frac{f_a(x) \times w(x,t)}{\int f_a(x) \times w(x,t)} \qquad (1)$$

where $f_a(x)$ is the null distribution of space use that models the probability of use in the absence of habitat selection (i.e., the availability distribution), and $w(x,t)$ is a selection function that transforms $f_a(x)$ to $f_u(x,t)$ by selectively weighting different areas based on habitat conditions (Johnson et al. 2008). We defined $f_a(x) = BVN(\theta)$ to be a stationary (i.e., time invariant) bivariate normal (BVN) distribution with parameters θ describing the means and variances in the x and y dimensions and the covariance. By describing $f_a(x)$ in this way, the areas considered available for selection can be thought of as a BVN distribution characterizing the entire home range of an individual. The BVN distribution characterizes the space use of an animal that biases movement towards a central place (Horne et al. 2008, Wilson et al. 2014b). We defined the selection function as:

$$w(x,t) = Exp\left[H(x)'\beta P(t)\right] \qquad (2)$$

where $H(x)'$ is a vector of covariate values describing the habitat or environmental conditions at location x, β is a vector of parameters (i.e., selection coefficients) to be estimated, and $P(t)$ is an interaction term representing functions of time (i.e., winter, summer) to allow for temporal variation in habitat selection. Others have used similar approach for modeling habitat selection through time (see Ferguson et al. 2000, Forester et al. 2009). We used maximum likelihood (via numerical optimization) to estimate the parameters governing the null model of home range (θ) and the selection coefficients (β) with a program written in R (R Development Core Team 2013) with code developed by J. Horne (see Slaght et al. 2013 for example code). We used odds ratios to aid interpretation of the estimated coefficients β_i. An odds ratio approximates the relative change in probability of event x occurring (e.g., a moose being present) given a 1-unit change in a given parameter (Hosmer and Lemeshow 1989).

Environmental variables

Based on previous research, we formulated 11 models to analyze seasonal habitat selection by moose (Table 1). Weixelman et al. (1998) and Maier et al. (2005) suggested that moose select habitats that burned 11–30 years prior to usage because these areas tend to revegetate with deciduous shrubs. Riparian zones often have abundant and high-quality forage that moose use in Alaska (Collins and Helm 1997, Maier et al. 2005, Stephenson et al. 2006). Areas with extensive vegetative cover typically have more deciduous trees (e.g., birch) and tall shrubs (e.g., willows) that are preferred moose forage than areas with low cover (e.g., tussock tundra). We expected moose to select areas that contained preferred forage, such as forested and burned habitat, and areas closer to rivers. The models that highlighted the importance of forage contained a mixture of covariates that included 'Fire' (if a moose was in habitat that burned 11–30 years prior to use), 'Forest' (if a moose used areas with extensive vegetative cover based on landcover type), and/or 'Dist_River' (distance from a riparian area; Table 1). We identified areas as 'fire' using the Alaska Fire Service's geodatabase which catalogs the extent, number, and location of large fires mapped from 1950–2014 (Fig. 2;

Table 1. Models and their structure used to analyze different hypotheses related to moose habitat selection in north-central Alaska, USA, 2008–2013.

Model	Covariates
Fire	Fire[a]
Forage	Fire+Dist_River[b]+Forest[c]
Predator	Dist_River+Forest
Terrain1	SRI[d]+Elev[e]
Terrain2	SRI+Slope
Terrain3	SRI+Elev+Elev^2
Terrain4	SRI+Slope+Slope^2
Complexity1	Fire+Forest+Dist_River+SRI+Elev
Complexity2	Fire+Forest+Dist_River+SRI +Slope
Complexity3	Fire+Forest+Dist_River+SRI+Elev +Elev^2
Complexity4	Fire+Forest+Dist_River+SRI +Slope+Slope^2

[a] 'Fire' denoted if a moose location was in habitat that burned 11-30 years prior to use

[b] 'Dist_River' is distance to a riparian area a moose was located

[c] 'Forest' denoted if a moose location was in habitat that was extensively vegetated (i.e. forest or tall shrubs)

[d] 'SRI' is a solar radiation index

[e] 'Elev' is elevation

data at http://fire.ak.blm.gov/predsvcs/maps.php), and 'forest' using the National Land Cover Database – Alaska 2001 coverage (http://www.epa.gov/mrlc/nlcd-2001.html). Major rivers were identified using the USGS 1:2,000,000 digital line graphs dataset (https://lta.cr.usgs.gov/DLGs).

We expected moose, particularly females with calves, to select areas further from riparian areas and that were more forested to reduce predation pressure. Riparian areas are often utilized by predators as travel corridors and forested areas provide more cover to hide from predators (Peterson 1995, Kunkel and Pletscher 1999, McPhee et al. 2012). Thus, we interpreted moose responses to riparian areas as a proxy for responding to areas of increased predation risk. The model highlighting the importance of predation pressure included the covariates of 'Dist_River' and 'Forest'.

Moose select areas based on physiography and 4 models were used to assess the importance of terrain including a mixture of the covariates slope, elevation and their squared terms (to assess non-linear relations), and 'SRI' (a solar radiation index, Keating et al. 2007; Table 1). These covariates were derived from our digital elevation model. Higher solar radiation is correlated with reduced snow depth during winter and increased net primary productivity (i.e., forage) during summer (Crabtree et al. 2009). We expected moose to select for terrain features that reduced snow depth, and subsequently increased forage availability, and that these patterns would be more prominent during more severe winters. We hypothesized that habitat selection by moose is influenced by a wide array of factors, rather than just forage abundance, predation pressure, or terrain acting alone. We used 4 models to assess this hypothesis, and covariates for these models included the entire suite used in the previous models.

We used remotely sensed data to quantify the spatial distribution of habitat covariates and included interaction terms between resource selection coefficients and functions of time (Ferguson et al. 2000, Forester et al. 2009) to account for temporal variation in habitat selection. Before modeling resource selection, we screened predictor variables for collinearity. We assumed that if $|r| < 0.60$, then correlation was not a concern between predictor covariates (Sawyer et al. 2006, Ciarniello et al. 2007). Slope and elevation were considered positively correlated and were not included together in any model.

Model selection

We used an information-theoretic approach for evaluating synoptic models of habitat selection and determined a set of *a priori* candidate models that we deemed biologically relevant (Burnham and Anderson 2002). We fit models to location data for each individual and year. We ranked the models for each moose and year using the difference in Akaike Information Criterion adjusted for small sample size (AIC_c) from the model with the smallest value (ΔAIC_c), and determined the relative likelihood of each model using Akaike weights (Burnham and Anderson 2002). Models, including the top model, which had an AIC_c score of <2 from the top model were designated as being in the top model set.

We evaluated habitat selection by sex, winter severity, and maternal status. We averaged estimates of selection coefficients across models based on Akaike weights for each individual and year. We scaled the weights to total 1 across models containing each variable (Burnham and Anderson 2002). For individuals that we observed during multiple years, we averaged the value of estimated-coefficients across years. To make class-level (i.e., sex, maternal status, and severity of the winter) inferences, we calculated the means and standard errors of univariate parameter estimates across all individuals for each parameter. If a parameter (e.g., fire) was not used by an individual, then no estimate was included for that individual for class-level inferences. For a conservative measure of precision at the class-level, we considered a coefficient to be significant if 2 times the standard error of the mean did not contain zero (Boyce 2006, Fieberg et al. 2010).

Complete separation of the data occurred where habitats were available but not used by a moose. For these individuals, we did not estimate a coefficient for the variable but simply noted avoidance (e.g., Nielsen et al. 2002). We entered elevation and slope as quadratic terms to allow for selection, or avoidance, at intermediate values of elevation and slope.

RESULTS

We retrieved 71,675 GPS locations from 37 moose between March 2008 and April 2013 via remote download and collar retrieval; 6 moose did not provide enough data to be included in our analyses. The remaining 31 moose (20 females and 11 males) produced 70 moose-years of data (range: 1–4 years per individual).

For male moose, the Complexity3 model (which included the covariates Fire, Forest, Dist_River, SRI, Elev, and $Elev^2$) best described habitat selection within home ranges during both winter and summer (Tables 1 and 2). Complexity3 was in the top model set for 48% and 46% of the individual moose-years during the winter and summer, respectively. Complexity1 was in the top model set for 29% and 38% of the individual moose-years during the winter and summer, respectively. Both Complexity4 and Terrain3 were in the top model set for 10% of the individual moose-years during the winter, and Complexity4 in the top model set for 8% of the individual moose-years during the summer. The remaining models were in the top model set for ≤10% of the individual moose-years during either season (Table 2).

For female moose, the Complexity3 model best described habitat selection within home ranges during both winter and summer (Tables 1 and 3). Complexity3 was in the top model set for 49% and 41% of the individual moose-years during the winter and summer, respectively. Complexity2 was in the top model set for 14% and 24% of the individual moose-years during the winter and summer, respectively. Terrain3 was in the top model set for 16% of the individual moose-years during the winter, and Complexity4 in the top model set for 16% of the individual moose-years during the summer.

Table 2. Top models of habitat selection by male moose in north-central, Alaska, USA, 2008–2013. The number of individual-years of data (n) for which each of the top 3 models of habitat selection received the most support, average and range of Akaike weights, and percent of times (%) each model occurred in the top model set (<2 AIC_c of the top model) are presented by season.

	Winter			Summer		
Model	n	Akaike weight	%	n	Akaike weight	%
Complexity3	10	0.95 (0.62–1.00)	48	11	0.85 (0.22–1.00)	46
Complexity1	6	0.92 (0.55–1.00)	29	9	0.77 (0.30–1.00)	38
Complexity4	2	0.69 (0.38–1.00)	10	2	0.47 (0.24–0.70)	8
Terrain3	2	1.00 (1.00–1.00)	10			

Table 3. Top models of habitat selection by female moose in north-central, Alaska, USA, 2008-2013. The number of individual-years of data (n) for which each of the top 3 models of habitat selection received the most support, average and range of Akaike weights, and percent of times (%) each model occurred in the top model set (<2 AIC_c of the top model) are presented by season.

	Winter			Summer		
Model	n	Akaike weight	%	n	Akaike weight	%
Complexity3	31	0.88 (0.32–1.00)	49	26	0.79 (0.25–1.00)	41
Complexity1	9	0.73 (0.27–1.00)	14	15	0.77 (0.27–1.00)	24
Complexity4				10	0.66 (0.17–0.98)	16
Terrain3	10	0.79 (0.23–1.00)	16			

The remaining models were in the top model set for ≤10% of the individual moose-years during either season (Table 3).

Nearly half (11 of 23) of the moose in the northern portion of the study area, where wildfire is less common than in the southern portion, did not use burned habitat during either winter or summer. All 8 moose in the southern portion of the study area used burned habitat, with 1 animal located only within burned habitat.

Seasonal selection patterns by moose

Patterns of selection by moose varied between season and sex (Table 4). Male moose consistently selected areas that were forested, lower in elevation, and with gentler slopes in winter; during summer they selected areas that were forested. During both seasons males were more variable in their selection of areas that received higher amounts of solar radiation, that were closer to riparian habitat, or that had been burned. Across seasons, female moose consistently selected areas that were forested, burned, and lower in elevation. Further, during winter females selected areas that received higher amounts of solar radiation, and during summer they avoided steeper slopes. Distance to riparian habitat was not consistently selected or avoided by females during either season.

Winter severity

The severity of the winter influenced habitat selection. As expected, moose selected areas lower in elevation with gentler slopes during more severe winters suggesting that snow depth influenced habitat selection. Based on average probability ratios, moose were 56% less likely to select a location for every 100 m higher during severe winters, but only 6% less likely during mild winters. In addition, moose selected areas closer to rivers during more severe winters. During mild

Table 4. Average parameter estimates (β) used to characterize selection by moose in north-central, Alaska, USA, 2008–2013. Bold values were significant at the class level (i.e., sex and population). Values in parentheses represent n for each class. 'F' denotes female and 'M' male.

	Winter		Summer		Winter	
	Male (11)	Female (20)	Male (11)	Female (20)	Mild (19 F, 8 M)	Mod/Severe (18 F,11M)
Fire[a,x]	−1.12	**1.37**	0.02	**3.57**	1.15	0.10
SRI[b]	−1.98	**0.70**	2.26	0.60	0.19	−0.64
Non-linear Elev[c]						
Elev	5.08	**35.89**	**65.27**	**52.71**	**50.68**	3.23
Elev^2	−30.66	**−86.05**	**−103.20**	**−114.05**	**−107.74**	−33.61
Non-linear Slope						
Slope	2.87	2.58	**12.53**	2.52	**5.12**	0.62
Slope^2	**−11.24**	−5.74	**−18.94**	**−13.66**	**−8.72**	**−7.09**
Dist_River[d]	−3.08	−1.18	−2.17	0.50	−0.25	−2.29
Forest[e]	**0.34**	**0.39**	**0.76**	**0.36**	**0.46**	**0.33**
Elev	**−22.38**	**−4.63**	−2.47	**−6.94**	−1.21	**−17.19**
Slope	**−3.67**	−0.89	0.41	**−2.85**	−0.32	**−2.73**

[a] 'Fire' denoted if a moose location was in habitat that burned 11–30 years prior to use
[b] 'SRI' is a solar radiation index
[c] 'Elev' is elevation
[d] 'Dist_River' is distance to a river a moose was located
[e] 'Forest' denoted if a moose location was in habitat that was extensively vegetated (i.e. forest or tall shrubs)
[x] Not all moose utilized recently burned habitat so sample sizes were: winter male, n=4; winter female, n=12; summer male, n=7; summer female, n=10

winters moose were more variable in their selection of most land-cover classes and landscape features (Table 4).

Maternal status

Six females successfully raised at least 1 calf through to the following spring, 11 lost calves by fall, and 11 either did not give birth or lost their calves during the first month post-birth. We were unable to determine the maternal status of 9 females. During both seasons, females with calves selected areas further from rivers, more forested, and with less burned habitat than females without calves (Table 5). For example, based on average probability ratios, females with calves were 20% more likely to select a site 1000 m further from a river, whereas females without calves were 13% less likely to be found there. Females with calves were 70% more likely to be in forested habitat, whereas females without calves were only 40% more likely to be there.

DISCUSSION

Similar to studies in other northern regions, we found that moose in north-central Alaska selected for habitats with extensive canopy cover. Where habitat that burned 11–30 years previous was available, moose, particularly females, selectively used it (presumably) because habitats at this seral stage tend to have abundant forage (MacCracken and Viereck 1990, Weixelman et al. 1998, Maier et al. 2005). This appears to support the hypothesis that moose habitat selection is primarily driven by availability of forage abundance and quality (Peek 1997). However,

Table 5. Average parameter estimates (β) used to characterize selection by maternal status of female moose in north-central, Alaska, USA, 2008–2013. Bold values were significant. Values in parentheses represent n for each class.

	Winter		Summer	
	Calf (6)	No Calf (22)	Calf (17)	No Calf (11)
Fire[ax]	−0.30	0.73	4.16	7.23
SRI[b]	0.14	0.39	0.41	0.58
Non-linear Elev[c]				
Elev	43.02	**39.93**	**31.59**	**47.95**
Elev²	−84.31	**−79.63**	**−95.45**	**−129.86**
Non-linear Slope				
Slope	2.47	2.31	0.63	4.93
Slope²	−1.79	−5.42	**−10.49**	**−17.71**
Dist_River[d]	1.62	−1.26	1.90	−0.59
Forest[e]	0.51	**0.34**	**0.38**	0.24
Elev	−3.26	−0.60	**−6.80**	−5.79
Slope	0.27	−0.52	**−3.24**	−1.13

[a] ‘Fire’ denoted if a moose location was in habitat that burned 11–30 years prior to use

[b] ‘SRI’ is a solar radiation index

[c] ‘Elev’ is elevation

[d] ‘Dist_River’ is distance to a river a moose was located

[e] ‘Forest’ denoted if a moose location was in habitat that was extensively vegetated (i.e. forest or tall shrubs)

[x] Not all moose utilized recently burned habitat so sample sizes were: winter calf, n=1; winter no calf, n=10; summer calf, n=2; summer no calf, n=7

this hypothesis was not supported by our top models that included the greatest number of variables. The majority (>66%) for both males and females included indices of forage abundance (time since last fire), extensive vegetative cover (forest), distance to river, in addition to elevation and solar radiation. While many of these covariates can be associated with forage abundance, our results suggest that a wide array of factors likely influence habitat selection by moose – supporting the hypothesis that habitat selection by moose is driven by a complex interaction of diverse factors.

We found that patterns of habitat selection differed between sex and season. Male and female moose exhibited similar patterns of selection for terrain features, particularly elevation during summer. During winter, however, sex-related differences were evident. As expected, males moved to lower elevations, but unexpectedly, females remained at similar elevations throughout the winter. This behavioral difference might provide smaller-bodied females some benefit of higher quality forage (i.e., in burned areas) and terrain features that reduced snow pack (i.e., higher SRI). However, predation on moose is often greater in lowland areas (Fuller and Keith 1980).

Within the region, wolves often travel along riparian corridors (Lake et al. 2013). We suspect that predators focus their hunting along riparian corridors, owing to the concentration of prey in areas of lower snow depth and that travel is probably easier for predators due to smooth, hard surfaces afforded by rivers (Peterson 1995, Kunkel and Pletscher 1999, McPhee et al. 2012). Moose reduce their vulnerability to wolf predation by avoiding areas used by wolves for travel (Kunkel and Pletscher 1999). Our findings are consistent with the hypothesis that females try to minimize predation risk, whereas males adopt a strategy to maximize forage intake (Fuller and Keith 1980, Oehlers et al. 2011).

Moose, with their large size and formidable strength, are well-adapted to snow (Telfer and Kelsall 1979, Peek 1997). Nevertheless, deep (65–70 cm) snow can affect moose movement, distribution, and home range size (van Ballenberghe 1977, Miquelle et al. 1992, Peek 1997, Ball et al. 2001, Joly et al. 2015b). As expected, during severe winters moose selected habitats that were at lower elevations, with gentler slopes, and closer to rivers than during mild winters. Deep snow at mid- to high elevations, or in early successional stages of burns, can cover preferred browse inducing moose to move to lower elevations and use areas where forage is more concentrated within riparian areas (Weixelman et al. 1998). Relatively higher moose densities in valley bottoms during severe winters may attract predators such as wolves, and thus increase localized predation risk (McPhee et al. 2012, Lake et al. 2013). Thus, harsh winters may have indirect, as well as direct, negative impacts on moose in our study area that may reduce their productivity and survivorship. We found that moose were more variable in their selection of land-cover classes and landscape features during mild winters, suggesting that tendencies for moose to select lower elevational areas closer to rivers during winter may be more related to snow depth, and subsequently, forage availability not forage quality.

Interestingly, we did not find that moose utilized habitats with higher canopy cover during severe winters which may reflect that many trees are diminutive in our high-latitude study area. Even though forest stands can have relatively high canopy cover, there may be insufficient overhead foliage to intercept snow and reduce underlying depths, or provide thermal cover.

We found that maternal status influenced patterns of habitat selection by females. As expected, females with calves avoided riparian habitats and selected areas with more forested habitat than females without calves during both summer and winter. In addition, females with calves selected areas with less burned habitat than females without calves. Both riparian habitat and burned areas tend to provide more high quality moose forage than other habitat types (Collins and Helm 1997, Maier et al. 2005, Stephenson et al. 2006). These results suggest that maternal status-related differences in habitat selection patterns were likely more related to the specific needs of females with regard to protection of calves. However, due to the small sample size of females with calves (n = 6), our results should be considered preliminary.

Habitat selection is fundamental to the ecology of wildlife species. Understanding patterns of habitat selection by moose can improve their management. An obvious example to use this information is to help guide where and when development occurs to minimize loss of critical moose habitat. Our work is timely, given that a proposed industrial road would bisect the study area (Wilson et al. 2014a, Guettabi et al. 2016). Further, enhanced knowledge of moose movements, distribution, and habitat selection should be useful to abate conflicts between subsistence and non-subsistence hunters by spatially or temporally separating users near high quality moose habitat.

The Arctic is undergoing rapid warming which will result in measurable ecological changes (Hinzman et al. 2005, IPCC 2007). Further, wildfire is predicted to increase in the region, potentially creating more productive foraging habitats for moose (Joly et al. 2012). By collecting baseline data on habitat selection and use, future researchers will be better able to assess the impacts of climate change on moose at their northern extent of range in North America.

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