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Boreal forest titans do not clash: low overlap in winter habitat selection by moose (*Alces americanus*) and reintroduced bison (*Bison bison*)

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Abstract

Despite moose (*Alces americanus*) likely being both an ecological and cultural keystone species in the North American boreal forest, few studies have examined niche overlap between moose and other ungulates. In response to concerns from local people about the potential for competition for habitat between moose and reintroduced bison (*Bison bison*), and the potential for disturbance to moose by bison and bison hunters, we investigated overlap in winter habitat selection by these species in southwestern Yukon, Canada. We used available geo-referenced data of animal locations, and associated environmental covariates, to develop resource selection probability function (RSPF) models of early-winter and late-winter habitat selection by moose and bison. In early-winter, moose selected sub-alpine shrub-dominated habitats, whereas bison extensively selected wet sedge meadows in lowland valleys. Both species used a greater variety of habitats in late-winter, with moose selecting drainages above tree line or river valleys with deciduous forest cover, while bison selected either south-facing grassy slopes or wet sedge meadows. Given observed differences in seasonal habitat selection between moose and bison, these species are predicted to overlap on only 0.5 and 6.6% of our 12,818-km^2 study area during early-winter and late-winter, respectively. The lack of demonstrated winter habitat overlap between moose and reintroduced bison, coupled with low diet overlap, points to an overall low potential for competition for winter habitat between these species, or for disturbance to moose attributable to bison or bison hunters. Resource partitioning that facilitates coexistence on a shared landscape suggests that concern over the impact of reintroduced bison on resident populations of moose is likely unwarranted.

Keywords *Alces americanus* · Bison · *Bison bison* · Habitat use · Niche overlap · Moose · Resource selection probability function · RSPF

Introduction

Moose (*Alces americanus*) are perhaps the most valued wildlife resource used by local people throughout the North American boreal forest. They are a key food source, and as one of the largest terrestrial mammals in northern forest ecosystems, they may contribute greatly to the food security of local communities. Importantly, moose also provide spiritual, cultural, recreational, and economic benefits to many northern

residents (reviewed by Timmerman and Rodgers (2005)). In addition, moose may be a keystone species in the ecology of boreal forests because of their influence on nutrient cycling (Pastor et al. 1988; Molvar et al. 1993) and vegetation succession (Kielland and Bryant 1998; Persson et al. 2000) and their importance in the diet of a host of predators and scavengers. As such, factors that may potentially limit or regulate their abundance have received considerable scientific attention, with research focused on predation (e.g., Gasaway et al. 1992; Messier 1994; James et al. 2004), climate change (e.g., Lowe et al. 2010; Broders et al. 2012), modifications to the landscape and habitat (e.g., Rempel et al. 1997; Collins and Schwartz 1998; Bowman et al. 2010), harvest sustainability (e.g., Crête et al. 1981; Sæther et al. 2001), and human disturbance (Colescott and Gillingham 1998; Lykkja et al. 2009).

Niche overlap between moose and other herbivores in North America, however, has received relatively cursory

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attention. Several investigations on niche overlap between moose and hare (*Lepus* spp.) have reported a high potential for competition for food resources (Dodds 1960; Wood 1974; Wolff 1980; Belovsky 1984). Surprisingly, less work has been done on resource overlap between moose and other ungulates (but see Telfer 1970; Jenkins and Wright 1988; Messier 1991; Cumming et al. 1996; Jung et al. 2015a, b), despite the fact that moose occur sympatrically with other ungulate species, such as deer (*Odocoileus* spp.), elk (*Cervus canadensis*), or caribou (*Rangifer tarandus*).

In response to concerns by local people (Government of Yukon 2012; Clark et al. 2016), we investigated niche overlap between moose and reintroduced bison (*Bison bison*) on a shared winter range in northwestern Canada. Bison were extirpated from much of northwestern North America by the turn of the nineteenth century (Soper 1941; Sanderson et al. 2008), and extensive recovery efforts ensued. In 1980, a program was initiated to reintroduce bison to southwestern Yukon, Canada, and the resultant population grew rapidly, producing unexpected management challenges (Jung et al. 2015a, b; Clark et al. 2016; Jung 2017). Despite bison formerly being indigenous to the region, local people had substantial concern over the impacts of reintroduced bison on resident moose, the latter of which they depend on as a cultural keystone species (sensu Garibaldi and Turner 2004). As such, a key management action arising from a community-based management plan for reintroduced bison in the region was to understand the potential impact of reintroduced bison on moose (Government of Yukon 2012).

Previously, Jung et al. (2015a) investigated dietary overlap between moose and bison during winter and confirmed that moose in our study area were a shrub specialist, with 99.8% of their winter diet at high elevations consisting of shrubs, predominately *Salix* spp. and *Betula* spp. Bison, on the other hand, had much more diverse winter diets that were largely composed of sedges (*Carex* spp.) and rushes (Jung 2015; Jung et al. 2015a). Consequently, winter dietary overlap between moose and reintroduced bison was found to be low to moderate (13–42%), suggesting low potential for exploitative competition for food resources (Jung et al. 2015a). However, a companion study investigated co-occurrence of bison and moose in late-winter and found that they both were present in 287 of 676 (42.5%) 12.2-km^2 cells surveyed, suggesting the potential for overlap in winter habitat use (Jung et al. 2015b). Bison are a popular species for hunters in winter, and given that moose react overtly to disturbance by snowmobiles (Colescott and Gillingham 1998; Harris et al. 2014), there was a concern by local people that hunters pursuing bison on snowmobiles would inadvertently create substantial disturbance to the resident moose (Clark et al. 2016). So the question remained whether the winter habitat preferences of these species

overlapped and the potential for competition and disturbance impacts that may ensue if they preferred similar habitats.

In this study, we examined winter habitat overlap between resident moose and reintroduced bison as a means of assessing the potential for competition for preferred habitats and disturbance impacts to moose created by reintroduced bison. We used available datasets of geo-referenced locations of bison and moose to develop habitat selection models, calculated habitat selection maps for each species, and identified areas of overlap in habitat preferences. While much work has been done on winter habitat selection by moose (e.g., Poole and Stuart-Smith 2006; Jung et al. 2009; Lenarz et al. 2011) and bison (e.g., Larter and Gates 1991), how these species partitioned habitats on a shared range remained unknown and was a source of angst for managers and local people (Government of Yukon 2012; Clark et al. 2016). We focused our analyses during winter, a time when food resources are most limited and niche overlap for northern ungulates may be greatest (Jenkins and Wright 1987; Jung et al. 2015b) and when hunters are actively pursuing bison. Given that moose are primarily browsers (e.g., Risenhoover 1989) and bison are primarily grazers (e.g., Larter and Gates 1991; Jung 2015), we predicted that they would use different habitats, where each would find preferred forage; thus, limiting overlap in habitat selection.

Methods

Study area

Our study was conducted in the Boreal Cordillera Ecozone (Wiken 1986), northwest of Whitehorse, Yukon, Canada (60.7° N, 135.1° W; Fig. 1). We defined our 12,818-km^2 study area by generating a 100% minimum convex polygon (MCP) around locations of global positioning system (GPS)-collared bison (see as follows) in a geographic information system (GIS) and buffering the area by 10 km. Elevation ranged from 502 to 2345 m above sea level (ASL), and much of the area was above tree line (approximately ≥ 1000 m ASL), with several mountain peaks ≥ 1600 m ASL and extensive alpine plateaus. Alpine areas were bisected by several large lakes, including Aishihik Lake and Taye Lake, and deeply incised river valleys. Vegetation at lower elevations and valley bottoms included open canopy white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) forest and dwarf willow (*Salix* spp.) and dwarf birch (*Betula nana*) shrublands, interspersed with mesic sedge (*Carex* spp.) meadows. Remnant boreal grasslands occurred as small patches on south-facing slopes and at low elevations (Vetter 2000). Alpine plant communities

were dominated by willow and dwarf birch, graminoids, and mosses. Climate was cold and semi-arid, with snow cover extending from early-October to mid-May.

Bison and moose were common but occurred in low densities in both alpine and lowland habitats (Jung et al. 2015a, b). However, populations of bison were increasing during our study and moose were presumed to be stable (Yukon Department of Environment, unpublished data). Jung et al. (2015b) provide more details on densities and winter distribution of ungulates in the study area. Humans hunting bison (primarily by snowmobile) used the study area extensively from November to March, with most hunting activity occurring in February and March (Yukon Department of Environment, unpublished data).

Ungulate location data

Bison spatial data were obtained from 16 adult female bison equipped with GPS collars from 2005 to 2009. Locations were collected hourly for GPS-collared bison (see Jung and Kuba (2015) for details). We excluded the first 3 days post-capture to negate potentially abnormal movement behavior and habitat choices that may have been a result of capture effects (e.g., Morellet et al. 2009; Neumann et al. 2011). We calculated the movement rate between locations and found that only 1% of the movement bouts were > 1.7 km/h. We visually inspected all locations above this threshold to assess inclusion in the final dataset. Bison were not faithful to specific wintering areas between years; therefore, we included multiple years of locations for individual bison where data were available. However, we restricted inclusion of a bison-season (one bison-season = one GPS-collared bison monitored for one season) if locations were not available for ≥ 80% of the length of the season (mid-November to mid-May). The remaining dataset consisted of 106,203 winter locations.

Geo-referenced locations of moose in our study area were obtained from aerial surveys of moose during 1993–2011 (Environment Yukon, unpublished data). Generally, aerial surveys were done from a helicopter (Bell 206B) by two observers, as Smits et al. (1994) showed that helicopter-based surveys of moose in Yukon were more accurate than those from faster flying fixed-wing airplanes. Protocols for the conduct of moose aerial surveys used in our study are provided by Smits et al. (1994) and Hayes et al. (2003). Specifically, surveys were flown at an altitude of 60–80 m above ground level (agl), with a search effort of 2 min/km^2, which Smits et al. (1994) showed resulted in detection of 97% of the moose in Yukon. Locations of moose observations were marked on 1:50,000 topographical maps, or, in later years, via an onboard or handheld GPS unit. Most moose surveys were completed by the same observer/navigators and pilots, reducing the potential for observer bias (Larsen 1982). Our dataset consisted of 1065 geo-referenced locations of moose in the study area

during winter. We estimated location error rates to be ≤ 30 and 30–100 m for bison and moose, respectively. Moose location error rates likely decreased substantially (< 50 m) after 2000, when aerial surveys utilized a GPS to mark locations and location error was not influenced by degradation of GPS-obtained coordinates because of selective availability.

Environmental covariates

Habitat covariates were extracted and mapped as layers within a GIS (Table 1). Vegetation maps were generated from Earth Observation for Sustainable Development of Forests (EOSD) base layers, which were based on Landsat 7 Enhanced Thematic Mapper Plus (ETM+) images, circa 2000 (Wulder et al. 2008). Vegetation types considered in the analysis included the percent of shrub, wetland, herbs (i.e., vascular plants such as grasses and forbs), and conifer and deciduous forest cover. A moving window analysis was applied at 100-m and 1-km radius scales using 25 × 25-m pixels to represent the percent of the vegetation type of interest within the specified extent (Table 1). Map layers depicting the distance to water sources were generated by extracting river and lake layers from digitized 1:50,000 topographic NTS (National Topographic Series) maps. Maps were rasterized to 25 × 25-m pixels to match the pixel size of EOSD maps, and the Euclidean distance from each cell to the nearest water source was calculated. Slope, aspect, and terrain ruggedness were derived from Digital Elevation Models (DEMs; geogratis. com) merged and resampled (from 30 × 30 to 25 × 25 m) to match other layers. Terrain ruggedness was calculated using a vector measure that quantified local variation in terrain, as per Sappington et al. (2007). Available habitat was represented by 20,000 random points within the study area (approximately 1. 5 points/km^2).

Habitat models

We used weighted distributions to estimate resource selection probability functions (RSPFs) in a use-availability design (Lele and Keim 2006; Lele 2009). An RSPF is a function that describes the probability that a particular resource, as described by a series of environmental covariates, will be selected by an individual animal (Manly et al. 2002). Advances in computational algorithms make it possible to estimate probability of selection with logistic regression models (Hosmer and Lemeshow 2000; Lele 2009), which provide stronger inferences compared to commonly used exponential RSF models that provide only relative probability of selection, and may not accurately represent natural processes, resulting in biased probability maps.

We divided the bison and moose datasets into two biologically relevant seasons, based on bison movement rates obtained from the GPS-collared animals: early-winter (11

Table 1   Habitat covariates used in seasonal resource selection probability function (RSPF) models of bison (*Bison bison*) and moose (*Alces americanus*) winter habitat selection in southwestern Yukon, Canada. The 'used' column refers to if the variable was included in RSPF models, after controlling for multicollinearity among covariates

Covariate	Used	Description	Variable type
Dist. water	Yes	Distance (m) to nearest lake or river based on 1:50,000 topographic maps	Continuous
Elevation	Yes	Elevation based on a Digital Elevation Model (DEM)	Continuous
Slope	Yes	Slope based on four categories, from DEM	Categorical
Aspect	Yes	Aspect based on four categories, from DEM	Categorical
Ruggedness	Yes	Terrain ruggedness index uncorrelated to elevation	0–1
% Shrub 100 m	No	% area covered by shrub within a 100-m radius	0–1
% Shrub 1 km	Yes	% area covered by shrub within a 1-km radius	0–1
% Herb 100 m	No	% grass, forb, graminoid within a 100-m radius	0–1
% Herb 1 km	Yes	% grass, forb, graminoid within a 1-km meter radius	0–1
% Decid. 100 m	No	% area covered by deciduous trees within a 100-m radius	0–1
% Decid. 1 km	Yes	% area covered by deciduous trees within a 1-km radius	0–1
% Conif. 100 m	No	% area covered by coniferous trees within a 100-m radius	0–1
% Conif 1 km	Yes	% area covered by coniferous trees within a 1-km radius	0–1
% Wetland 100 m	No	% area covered by wetlands within a 100-m radius	0–1
% Wetland 1 km	No	% area covered by wetlands within a 1-km radius	0–1

November–31 January) and late-winter (1 February–13 May). A manual stepwise model building procedure was used, whereby individual covariates were visually screened and only those covariates with biologically relevant selection relationships were considered as potential covariates in seasonal models. Model selection was based on forward stepwise inclusion where prescreened covariates were added sequentially in order of their strength in explaining the data based on Akaike information criterion (AIC; Burnham and Anderson 2002) and visual inspection. We considered this approach appropriate, as models would be used for predictive purposes. RSPF estimation requires at least one continuous covariate; thus, estimation of seasonal models where the best two covariates were categorical required the addition of the next best continuous covariate. When covariates were highly correlated ($r > 0.6$), we only considered the variable that provided the better fit to avoid collinearity issues (Hosmer and Lemeshow 2000), except in cases there was high multicollinearity between variables and similar predictive value. When biologically appropriate, we also tested the fit of second order transformations. This pluralistic approach incorporates advantages of hypothesis testing and information theory (Stephens et al. 2005, 2007).

We identified the most parsimonious models based on AIC, using a threshold of 10, for distinguishing differences in models (Burnham and Anderson 2002), area under the receiver operating characteristic curve (AUC) to measure model discrimination, and variance inflation factor (VIF) to assess level of correlation between predictors, with VIF values < 10 being considered acceptable (O'Brien 2007). AUC graphs plot true positives (sensitivity) versus false positives (1-specificity) for a binary classifier system, as its discrimination threshold is varied. Therefore, a model with no discriminating power would have an AUC value of 0.5. Generally, AUC values between 0.7 and 0.8 are considered to have acceptable discrimination and values above 0.8 are considered to be excellent (Hosmer and Lemeshow 2000). Models with the lowest AIC score and highest AUC are considered the best fit to the data.

Habitat overlap

We assumed that areas of high selection were biologically important (Railsback et al. 2003) and identified high-quality habitats based on RSPF models. We partitioned the study area into three bins based on an equal area classification, representing low, medium, and high selection areas for bison and moose. Early-winter and late-winter habitat selection maps were generated for bison and moose using the top RSPF model. To quantify the percent of overlap between bison and moose, we compared areas with a high probability of habitat selection for both species.

Results

Winter habitat selection

During the early-winter, bison spent most of their time (96.4% of the locations) below the tree line, on flat terrain at elevations between 600 and 900 m ASL. The most

parsimonious habitat selection model for bison during early-winter (M4, Table 2) had excellent discrimination (AUC = 0.83) and low VIF (1.7). During this season, bison selected wetland-conifer complexes and, more specifically, areas close to water (Table 3). Bison avoided patches with more than 40% shrub cover at the 1-km scale.

The most parsimonious habitat selection model for moose during early-winter (M1, Table 2) also had excellent discrimination power (AUC = 0.82) and low VIF (1.1). During this season, moose selected shrub habitats between 1200 and 1500 m ASL and avoided conifer forests. Moose also selected areas with slopes of 5–20° but did not show selection for any aspect (Table 3).

In late-winter, bison also spent most of their time (89.7% of the locations) at lower elevations (700–900 m ASL). The most parsimonious habitat selection model during late-winter (M5, Table 4) had adequate discrimination (AUC = 0.79) and acceptable VIF level (2.7). During this season, bison predominantly selected areas rich in graminoids, on south-facing slopes of approximately 15–25°, and secondly for flat areas near lakes in wetland/conifer mosaics; they avoided deciduous forests (Table 5).

Moose habitat selection was less specific during late-winter than during the early-winter. Our best model for late-winter (M4, Table 4) had weaker discrimination than in early-winter (0.68), but a low VIF level (1.1). Selection was the greatest for areas with a high proportion of deciduous forest at the 1-km scale and close to rivers. A wide range of elevations between 1000 and 1500 m ASL was also selected by moose, as were areas with greater than 20% shrub cover at the 1-km scale; areas where coniferous forest cover was greater than 20% at the 1-km scale were avoided (Table 5).

Habitat overlap

In our study area, habitat overlap for moose and bison in winter was minimal. In both early-winter and late-winter, bison and moose selected distinct vegetation types and did not overlap much in their habitat choices. In early-winter, bison largely used wetland-conifer complexes below 900 m ASL and avoided sites with more than 40% shrub cover. In contrast, moose selected shrub habitats between 1200 and 1500 m ASL and avoided conifer forests (Table 3). In late-winter, bison generally avoided deciduous forest areas whereas this vegetation type was the strongest predictor of moose habitat selection (Table 5). Given differences in seasonal habitat selection between moose and bison, these species are predicted to overlap on only 0.5 and 6.6% of the study area during early-winter and late-winter, respectively, based on the most highly selected third of the study area by each species (Fig. 1). Bison occasionally moving to higher elevations in late-winter resulted in greater habitat overlap with moose, compared to early-winter, but this overlap was minimal in our study area.

Discussion

Despite moose likely being a cultural and ecological keystone species in the North American boreal forest, this study is one of only a few that has examined overlap in habitat preference between moose and another ungulate in this vast region. Our main finding is that there was minimal overlap in

Table 2 RSPF models of early-winter habitat selection by bison (*Bison bison*) and moose (*Alces americanus*) in southwestern Yukon, Canada. RSPF models were based on forward stepwise procedures. Covariates are listed in order of their explanatory strength. AIC, AUC, and maximum VIF are test values used to assess the relative strength of each model

a) Bison

Model	Distance to water (m)	Wetland 100 m (%)	Slope (°)	Elevation (m)	Conifer 100 m (%)	Shrubs 1 km (%)	Aspect	AIC	AUC	Max. VIF
M1	X	X	X					−64,870	0.82	1.1
M2	X	X	X	X				−65,443	0.82	1.2
M3	X	X	X	X	X			−65,987	0.82	1.4
M4	X	X	X	X	X	X		−67,288	0.83	1.7
M5	X	X	X	X	X	X	X	−67,099	0.83	1.8

b) Moose

Model	Elevation (m)	Shrubs 100 m (%)	Conifer1 km (%)	Slope (°)	AIC	AUC	Max. VIF
M1	X	X			−557	0.82	1.1
M2	X		X		−453	0.79	2.3
M3	X	X	X		−557	0.82	2.3
M4	X	X			−566	0.82	2.3
M5	X		X	X	−472	0.80	2.6

Table 3 Coefficients (estimates), standard errors (SE), and test statistics (*z* and Pr values) for covariates in the highest ranked (shaded in Table 2) early-winter RSPF models of bison (*Bison bison*) and moose (*Alces americanus*) habitat selection in southwestern Yukon, Canada

Bison model 4					Moose model 4				
Covariate	Estimate	SE	*z* value	Pr(>|z|)	Covariate	Estimate	SE	*z* value	Pr(>|z|)
(Intercept)	1.519	0.052	29.5	< 0.001	(Intercept)	− 53.470	7.354	− 7.3	< 0.001
Dist. Water	− 1.332	0.024	− 55.8	< 0.001	Elevation	55.767	5.925	9.4	< 0.001
%Wetland 100 m	108.197	2.258	47.9	< 0.001	Elevation^2	− 19.242	2.161	− 8.9	< 0.001
Slope	− 0.124	0.003	− 46.3	< 0.001	%Shrub 100 m	1.902	0.220	8.6	< 0.001
Elevation	− 2.436	0.048	− 50.7	< 0.001					
%Conifer 100 m	4.498	0.082	54.8	< 0.001					
(%Conifer 100 m)^2	− 5.684	0.090	− 63.3	< 0.001					
%Shrub 1 km	− 1.888	0.042	− 45.3	< 0.001					

habitat selection between moose and reintroduced bison on a shared winter range, based on RSPF models and resultant habitat selection maps that predicted ≤ 6.6% of the landscape was highly suitable for both species during winter.

It is important to emphasize, however, that our study did not consider other seasons (e.g., summer); thus, the possibility of habitat overlap in those seasons remains. Nevertheless, we do not expect substantially greater habitat overlap in summer because moose and bison diets were also significantly different during summer (Jung et al. 2015a), and forage availability is likely not as limited during summer as it is in winter.

Another possible limitation of our study is the difference in data quality (location accuracy) between the two species obtained from the field data. Our moose location data were likely not as accurate as the bison location data,

and this may have resulted in some inaccuracies in vegetation types associated with moose location data. However, given the large difference in habitat use between the two species indicated by our RSPF and predicted habitat overlap models, it is unlikely that the potential difference in location error between the two datasets influenced our findings to a great degree.

Winter habitat selection by moose and bison in our study were in general agreement with previous, separate studies of moose (e.g., Molvar and Bowyer 1994) and bison (e.g., Larter and Gates 1991) habitat use in northwestern Canada and Alaska. Our RSPF models demonstrated that moose and bison were spatially segregated on the landscape along two primary axes: elevation and vegetation type. Most winter bison locations were below the tree line and in mesic areas, whereas moose in winter were most often above tree line in vast alpine

Table 4 RSPF models of late-winter habitat selection by bison (*Bison bison*) and moose (*Alces americanus*) in southwestern Yukon, Canada. RSPF models were based on forward stepwise procedures. Covariates are listed in order of their explanatory strength. AIC, AUC, and maximum VIF are test values used to assess the relative strength of each model

a) Bison

Model	Herbs 100 m (%)	Distance to lakes (m)	Wetland 100 m (%)	Aspect	Greenness	Shrubs 100 m (%)	Slope	AIC	AUC	Max. VIF
M1	X	X	X					− 54,664	0.77	1.1
M2	X	X	X	X				− 57,918	0.77	2.6
M3	X	X	X	X	X			− 63,641	0.79	2.6
M4	X	X	X	X		X		− 59,441	0.78	2.6
M5	X	X	X	X	X		X	− 63,732	0.79	2.7

b) Moose

Model	Deciduous 1 km (%)	Conifer 1 km (%)	Distance to rivers (m)	Shrubs 1 km (%)	AIC	AUC	Max. VIF
M1	X	X			− 245	0.65	1.1
M2	X		X		− 215	0.63	1.0
M3	X			X	− 155	0.60	1.1
M4	X	X	X		− 326	0.68	1.1
M5	X	X		X	− 243	0.65	1.2

Table 5   Coefficients (estimates), standard errors (SE), and test statistics (*z* and Pr values) for covariates in the highest ranked (shaded in Table 4) late-winter RSPF models of bison (*Bison bison*) and moose (*Alces americanus*) habitat selection in southwestern Yukon, Canada

Bison model 5				Moose model 4				
Covariate	Estimate	SE	*z* value	Pr(>|z|)	Covariate	Estimate	SE	*z* value	Pr(>|z|)
(Intercept)	− 2.002	0.139	− 14.3	< 0.001	(Intercept)	− 3.440	3.823	− 0.9	0.368
%Herb 100 m	5.882	0.345	17.1	< 0.001	%Decid. 1 km	4.686	0.696	6.7	< 0.001
Dist. Lakes	− 0.225	0.014	− 16.3	< 0.001	%Conifer 1 km	− 2.214	0.218	− 10.1	< 0.001
%Wetland 100 m	9.851	9.633	1.0	0.307	Dist. rivers	− 0.678	0.084	− 8.1	< 0.001
Aspect east	0.509	0.105	4.9	< 0.001					
Aspect south	1.335	0.105	12.7	< 0.001					
Aspect west	1.174	0.122	9.6	< 0.001					
Aspect flat	0.653	0.179	3.6	< 0.001					
Greenness	− 4.075	0.434	− 9.4	< 0.001					
Slope low	− 0.292	0.044	− 6.7	< 0.001					
Slope med	0.240	0.078	3.1	0.002					
Slope steep	− 0.307	0.210	− 1.5	0.144					

plateaus that maintained dense stands of shrubs. Areas highly selected by both species occurred as large continuous patches on the landscape. These species-specific habitat choices are in keeping with the forage preferences of moose and bison, with moose preferring shrubs and bison preferring sedges (Risenhoover 1989; Larter and Gates 1991; Jung 2015; Jung
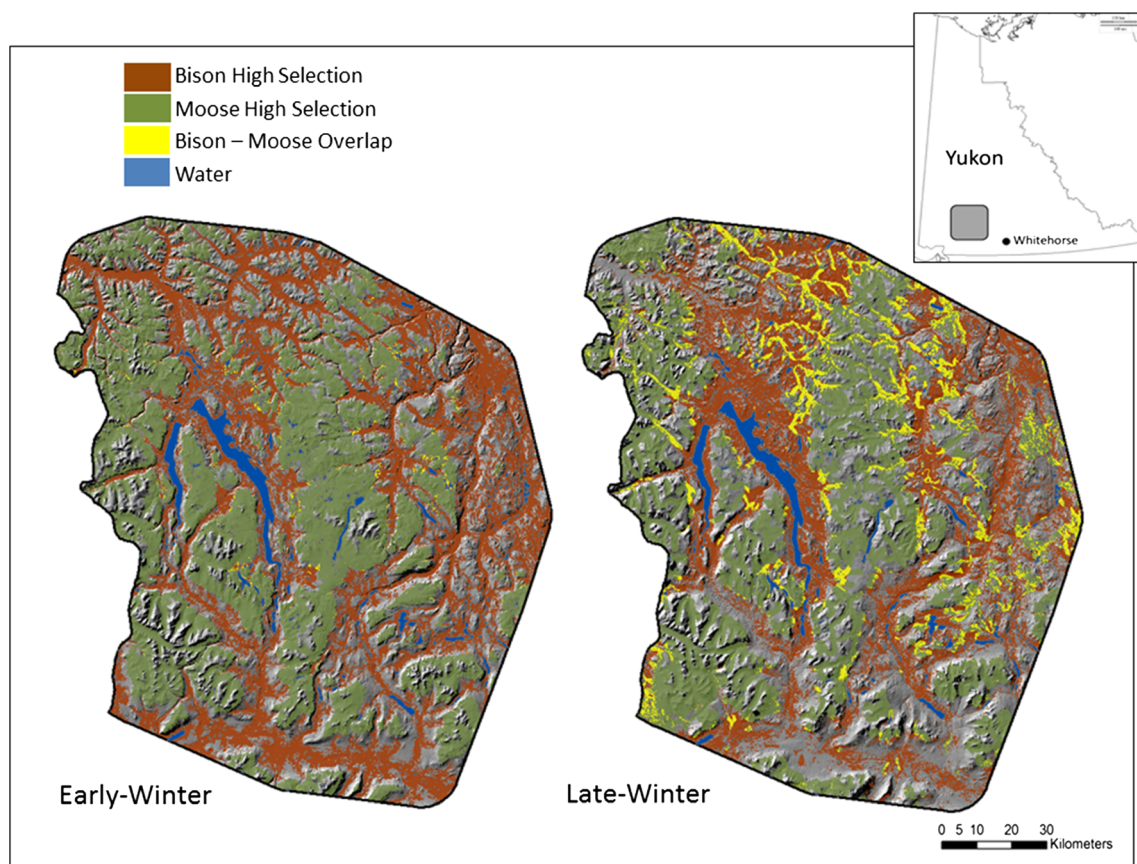

Fig. 1 Areas of predicted high habitat selection for reintroduced bison (*Bison bison*; brown shading) and moose (*Alces americanus*; green shading) and their overlap (yellow shading) during early-winter (left panel) and late-winter (right panel) in southwestern Yukon, Canada. Grey shading represents areas that were not predicted to be highly suitable habitat for either species. Areas of predicted high habitat selection represent the top third of suitable habitat, based on three equal sized bins from RSPF models (see text for details). Shaded square in the map inset is the location of the study area (Color figure online)

et al. 2015a). Clearly, moose and bison were selecting winter habitat, in part, that provided access to sufficient forage, and differences in their diets resulted in different habitat choices by the two species.

Our findings are consistent with other studies that examined habitat use by sympatric moose and other indigenous ungulates and found little overlap in winter; for example, woodland caribou (Cumming et al. 1996), white-tailed deer (*Odocoileus virginianus*; Telfer 1970), and elk (Jenkins and Wright 1988). None of these studies reported substantial winter habitat overlap between those resident ungulates and moose. For instance, Telfer (1970) reported that moose and white-tailed deer occupied exclusive winter habitat in New Brunswick, sharing only 1% of his study area. Similarly, in a 4-year snow-tracking study in Ontario, Cumming et al. (1996) reported habitat overlap by caribou and moose in only 2.3–5.8% of the 697 cells they surveyed.

It has been suggested that similar-sized ungulates may partition resources the least, compared to other species pairs (Jenkins and Wright 1988; Gordon and Illius 1989). Moose and bison are the largest land mammals in the boreal forest and similar in body size. Lack of resource overlap between these species in our study does not support the "similar body size" hypothesis, but is consistent with the hypothesis that similarity in ecophysiological characteristics (e.g., functional foraging mode, Hofmann 1989) is the primary predictor of competition among sympatric ungulates. As a shrub specialist (e.g., Risenhoover 1989; Jung et al. 2015a), moose are an extreme browser on the grazer-intermediate-browser scale (Hofmann 1989), while bison are primarily a grazer (Larter and Gates 1991; Jung 2015). Given these differences, it is not surprising that moose and bison select different habitats. Most other ungulates in the region are intermediate feeders (Jung et al. 2015a) and might be expected to overlap the niche of moose more so than a grazer such as bison. In fact, the greatest potential competitor for food and habitat resources with moose in our study area may be snowshoe hare (*Lepus americanus*), given that both species are shrub specialists in winter (Dodds 1960; Wolff 1980; Belovsky 1984).

The potential impact of reintroduced bison on resident moose has been an impediment to bison restoration across their historical range. Bison are the largest terrestrial mammal in North America, and they are gregarious. As such, it is not surprising that local people would be concerned about impact of reintroduced bison on resident wildlife, with a sharp focus on those species that are locally important, such as moose (Clark et al. 2016). Our study provides new insight on winter habitat overlap and hence the impact of competition or disturbance created by reintroduced bison and bison hunters on moose. However,

niche overlap is only relevant when considering the potential for exploitation competition, which was the main issue of concern regarding the impact of reintroduced bison on moose (Clark et al. 2016). Other types of competition (interference and apparent) may occur. Jung et al. (2015a) explored the potential for interference competition in winter between bison and moose in our study area and failed to find evidence that reintroduced bison effected the spatial distribution of moose at a medium spatial scale (12.2-km^2 cells). However, Larter et al. (1994) suggested that apparent competition between reintroduced bison and moose in the Northwest Territories may occur. We did not investigate this type of competition, and wolves (as well as humans) in our study area do prey on both moose and bison (Jung 2011). Further work to assess the occurrence and impact of apparent competition between reintroduced bison and moose may be necessary, if moose populations decline. However, data from Alaska suggests that moose densities are relatively high where bison and moose are sympatric, compared to elsewhere (C.T. Seaton, pers. comm.). In conclusion, our study, coupled with those by Jung et al. (2015a, b), suggests that the concern over exploitation or interference competition over scarce resources (food, habitat) between reintroduced bison and moose is likely unwarranted, as is the concern for disturbance to moose created by reintroduced bison or bison hunters, given distinctly different winter habitat choices by these two species.

References

Belovsky GE (1984) Moose and snowshoe hare competition and a mechanistic explanation from foraging theory. Oecologia 61:150–159

Bowman J, Ray JC, Magoun AJ, Johnson DS, Dawson FN (2010) Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Can J Zool 88:454–467

Broders HG, Coombs AB, McCarron JR (2012) Ecothermic responses of moose (*Alces alces*) to thermoregulatory stress on mainland Nova Scotia. Alces 48:53–61

Burnham KP, Anderson DR (2002) Model selection and multimodal inference, Second edn. Springer–Verlag, New York

Clark DA, Workman L, Jung TS (2016) Impacts of reintroduced bison on First Nations people in Yukon, Canada: finding common ground through participatory research and social learning. Conserv Soc 14(1):12

Colescott JH, Gillingham MP (1998) Reaction of moose (Alces alces) to snowmobile traffic in the Greys River Valley, Wyoming. Alces 34: 120–125

Collins WB, Schwartz CC (1998) Logging in Alaska's boreal forest: creation of grasslands or enhancement of moose habitat. Alces 34: 355–374

Crête M, Taylor RJ, Jordan PA (1981) Optimization of moose harvest in southwestern Quebec. J Wildl Manag 45:598–611

Cumming HG, Beange DB, Lavoie G (1996) Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer 9:81–94

Dodds DG (1960) Food competition and range relationships of moose and snowshoe hare in Newfoundland. J Wildl Manag 24:52–60

Garibaldi A, Turner N (2004) Cultural keystone species: implications for ecological conservation and restoration. Ecol Soc 9(3):1

Gasaway WC, Boertje RD, Grangaard DV, Kellyhouse DG, Stephenson RO, Larsen DG (1992) The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildl Monogr 120:1–59

Gordon IJ, Illius AW (1989) Resource partitioning by ungulates on the Isle of Rhum. Oecologia 78:383–389

Government of Yukon (2012) Management plan for the Aishihik wood bison (Bison bison athabascae) herd in southwestern Yukon. Environment Yukon, Whitehorse

Harris GH, Nielson RM, Rinaldi T, Lohuis T (2014) Effects of winter recreation on northern ungulates with focus on moose (Alces alces) and snowmobiles. Eur J Wildl Res 60:45–58

Hayes RD, Farnell R, Ward RMP, Carey J, Dehn M, Kuzyk GW, Baer AM, Gardner CL, O'Donoghue M (2003) Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildl Monogr 152:1–35

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 79:443–457

Hosmer DW, Lemeshow S (2000) Applied logistic regression, 2nd edn. Wiley, New York

James ARC, Boutin S, Hebert DM, Rippin AB (2004) Spatial separation of caribou from moose and its relation to predation by wolves. J Wildl Manag 68:799–809

Jenkins KJ, Wright RG (1987) Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. Can J Zool 65:1397–1401

Jenkins KJ, Wright RG (1988) Resource partitioning and competition among cervids in the northern Rocky Mountains. J Appl Ecol 25: 11–24

Jung TS (2011) Gray wolf (Canis lupus) predation and scavenging of reintroduced American bison (Bison bison) in southwestern Yukon. Northwest Nat 92:126–130

Jung TS (2015) Winter diet of reintroduced bison (Bison bison) in northwestern Canada. Mamm Res 60:385–391

Jung TS (2017) Extralimital movements of reintroduced bison (Bison bison): implications for range expansion and human-wildlife conflicts. Eur J Wildl Res 63:35

Jung TS, Kuba K (2015) Performance of GPS collars on free-ranging bison (Bison bison) in northwestern Canada. Wildl Res 42:315–323

Jung TS, Chubbs TE, Jones CG, Phillips FR, Otto RD (2009) Winter habitat selection of a low-density moose (Alces americanus) population in central Labrador. Northeast Nat 16:471–480

Jung TS, Stotyn SA, Czetwertynski SM (2015a) Dietary overlap and potential for competition in a dynamic ungulate community in northwestern Canada. J Wildl Manag 79:1277–1285

Jung TS, Hegel TM, Stotyn SA, Czetwertynski SM (2015b) Co-occurrence of resident and reintroduced ungulates on a shared winter range in northwestern Canada. Écoscience 22:7–16

Kielland K, Bryant J (1998) Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. Oikos 82:377–383

Larsen DG (1982) Moose inventory in southwest Yukon. Alces 18:142–167

Larter NC, Gates CC (1991) Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. Can J Zool 69:2677–2685

Larter NC, Sinclair ARE, Gates CC (1994) The response of predators to an erupting bison, Bison bison athabascae, population. Can Field Nat 108:318–327

Lele SR (2009) A new method for estimation of resource selection probability function. J Wildl Manag 73:122–127

Lele SR, Keim J (2006) Weighted distributions and estimation of resource selection probability functions. Ecology 87:3021–3028

Lenarz MS, Wright RG, Schrage MW, Edwards AJ (2011) Compositional analysis of moose habitat in northeastern Minnesota. Alces 47:135–149

Lowe SJ, Patterson BR, Schaefer JA (2010) Lack of behavioral responses of moose (Alces alces) to high ambient temperatures near the southern periphery of their range. Can J Zool 88:1032–1041

Lykkja ON, Solberg EJ, Herfindal I, Wright J, Rolandsen CM, Hanssen MG (2009) The effects of human activity on summer habitat use by moose. Alces 45:109–124

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals; statistical design and analysis for field studies, 2nd edn. Kluwer Academic Publishers, Dordrecht

Messier F (1991) The significance of limiting and regulating factors on the demography of moose and white-tailed deer. J Anim Ecol 60: 377–393

Messier F (1994) Ungulate population models with predation: a case study with the North American moose. Ecology 75:478–488

Molvar EM, Bowyer RT (1994) Costs and benefits of group living in a recently social ungulate: the Alaskan moose. J Mamm 75:621–630

Molvar EM, Bowyer RT, Van Ballenberghe V (1993) Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472–479

Morellet N, Verheyden H, Angibault J-M, Cargnelutti B, Lourtet F, Hewison MAJ (2009) The effect of capture on ranging behaviour and activity of the European roe deer (Capreolus capreolus). Wildl Biol 15:278–287

Neumann W, Ericsson G, Dettki H, Arnemo JM (2011) Effect of immobilizations on the activity and space use of female moose (Alces alces). Can J Zool 89:1013–1018

O'Brien RM (2007) A caution regarding rules of thumb for variance inflation factors. QualQuant 41:673–690

Pastor J, Naiman RJ, Dewey B, McInnes P (1988) Moose, microbes, and the boreal forest. Bioscience 38:770–777

Persson I, Danell K, Bergstrom R (2000) Disturbance by large herbivores in boreal forests with special reference to moose. Ann Zool Fenn 37: 251–263

Poole KG, Stuart-Smith K (2006) Winter habitat selection by female moose in western interior montane forests. Can J Zool 84:1823–1832

Railsback SF, Stauffer HB, Harvey BC (2003) What can habitat preference models tell us? Tests using a virtual trout population. Ecol Appl 13:1580–1594

Rempel RS, Elkie PC, Rodgers AR, Gluck MJ (1997) Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. J Wildl Manag 61:517–524

Risenhoover KL (1989) Composition and quality of moose winter diets in interior Alaska. J Wildl Manag 53:568–577

Sæther B-E, Engen S, Solberg EJ (2001) Optimal harvest of age-structured populations of moose *Alces alces* in a fluctuating environment. Wildl Biol 7:171–179

Sanderson EW, Redford KH, Weber B, Aune K, Baldes D, Berger J, Carter D, Curtin C, Derr JN, Dobrott S, Fearn E, Fleener C, Gerlach C, Gates CC, Gross JE, Gogan PJ, Grassel SM, Hilty JA, Jensen M, Kunkel K, Lammers D, List R, Minkowski K, Olson T, Pague C, Robertson PB, Stephenson RO (2008) The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. Conserv Biol 22:252–266

Sappington JM, Longshore KM, Thompson DB (2007) Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. J Wildl Manag 71:1419–1426

Smits CMM, Ward RMP, Larsen DG (1994) Helicopter or fixed-wing aircraft: a cost-benefit analysis for moose surveys in Yukon Territory. Alces 30:45–50

Soper JD (1941) History, range and home life of the northern bison. Ecol Monogr 11:347–412

Stephens PA, Buskirk SW, Hayward GD, Del Rio CM (2005) Information theory and hypothesis testing: a call for pluralism. J Appl Ecol 42:4–12

Stephens PA, Buskirk SW, Hayward GD, Del Rio CM (2007) A call for pluralism answered. J Appl Ecol 44:461–463

Telfer ES (1970) Winter habitat selection by moose and white-tailed deer. J Wildl Manag 34:553–559

Timmerman HR, Rodgers AR (2005) Moose: competing and complementary values. Alces 41:85–120

Vetter MA (2000) Grasslands of the Aishihik-Sekulmun Lakes area, Yukon Territory, Canada. Arctic 53:165–173

WikenEB (1986) Terrestrial ecozones of Canada. Ecological Land classification series. No. 19. Environment Canada. Ottawa, Ont

Wolff JO (1980) Moose-snowshoe hare competition during peak hare densities. Alces 16:238–254

Wood TJ (1974) Competition between Arctic hares and moose in Gros Morne National Park, Newfoundland. Alces 10:215–237

Wulder MA, White JC, Cranny M, Hall RJ, Luther JE, Beaudoin A, Goodenough DG, Dechka JE (2008) Monitoring of Canada's forests. Part 1: completion of the EOSD land cover project. Can J Remote Sens 34:549–562

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