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The role of vegetation structure in controlling distributions of vertebrate herbivores in Arctic Alaska

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A B S T R A C T

Climate-driven shrub expansion is altering the distribution of animal communities in the Arctic. A better understanding of habitat requirements is needed to accurately predict the response of herbivore communities to shrub expansion. We examined patterns of browsing by moose (*Alces alces*), snowshoe hare (*Lepus americanus*), and ptarmigan (*Lagopus lagopus, L. muta*) across the tundra of northern Alaska to determine whether forage requirements explain the distribution of herbivores in this ecosystem. In addition, we examined the potential for competition among these three shrub-dependent species. We recorded shrub characteristics and browsing levels at 59 sites along a 568 km riparian transect spanning from the Brooks Range to the Arctic Coast. Mean shrub height was positively correlated with browsing intensity for all three species (r = 0.40–0.71). The minimum shrub height threshold for hare occurrence (≥87 cm, 95% CI: 67–94) was similar to that for moose (≥81 cm, 95% CI: 65–96), whereas ptarmigan were nearly ubiquitous (≥3 cm, lower 95% CI = 0). Diet overlap among herbivores was nearly complete, with all three species heavily browsing feltleaf willow (*Salix alaxensis*). Our findings indicate that unlike moose and ptarmigan, forage availability does not appear to control the distribution of snowshoe hares in the Arctic. Resource competition may further affect distribution patterns within this guild as shrub cover continues to expand.

Introduction

The rate of warming in the Arctic is increasing faster than the global average (Chapman and Walsh, 2007; Bergengren et al., 2011; Serreze and Barry, 2011; IPCC, 2013). A warming climate is having acute impacts on biological and physical systems (Callaghan et al., 2004), including increased vegetation productivity (Bhatt et al., 2010; Elmendorf et al., 2012; Epstein et al., 2012), thawing permafrost (Liljedahl et al., 2016), and decreasing sea ice extent (IPCC, 2013). In response, species range shifts have been observed across taxonomic groups and geographic locations worldwide (Parmesan, 1996; Walther et al., 2002; Chen et al., 2011). In the Arctic, many species are observed or predicted to be undergoing northward range shifts, including marine organisms (Fossheim et al., 2015) and terrestrial species of

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plants (Tape et al., 2006; Danby and Hik, 2007; Pearson et al., 2013), insects (Jepsen et al., 2011), birds (Boelman et al., 2015), and mammals (Baltensperger and Huettmann, 2015; Tape et al., 2016a, 2016b).

Range shifts can directly alter interspecific interactions at multiple trophic levels (Tylianakis et al., 2008; Lancaster et al., 2017) and change community structures (Chapin et al., 1995; Pounds et al., 1999; Sagarin et al., 1999; LeRoux and McGeoch, 2008; Post et al., 2009). For example, recent shrub expansion in the Arctic (Tape et al., 2006) altered wildlife communities by improving habitat for shrub-dependent species (Ehrich et al., 2012; Henden et al., 2013) and potentially reducing habitat quality for previously existing species (Joly et al., 2012; Boelman et al., 2015).

Understanding distribution and possible colonization patterns of browsers is critical to predict arctic ecosystems' response to shrub expansion (Bryant et al., 2014). The central trophic position of herbivores facilitates their strong influence on the biodiversity of both predators and primary producers (Post and Pedersen, 2008; Kaarlejärvi et al., 2015) and ecosystem functioning (Schmitz, 2008; Väisänen et al., 2014). Additionally, many herbivore species, especially moose (*Alces alces*), are a valuable subsistence food source for human communities (Nelson et al., 2008; Titus et al., 2009).

Minimum habitat requirements for shrub-dependent vertebrates along the leading edge of their expanding ranges in the Arctic have not been quantified. The goal of this study was to quantify shrub habitat requirements and understand colonization patterns of vertebrate herbivores on the North Slope of Alaska. We examined shrub characteristics and patterns of browsing by three vertebrate herbivores: moose, snowshoe hare (*Lepus americanus*), and ptarmigan (*Lagopus lagopus, L. muta*). Ptarmigan have been historically the primary browsers in the Arctic (West and Meng, 1966), whereas moose and snowshoe hares have recently expanded their northernmost ranges onto the North Slope of Alaska (Tape et al., 2016a, 2016b). Browsing by these herbivores can strongly affect vegetation communities (Butler et al., 2007; Christie et al., 2014) and ecosystem level processes through changes in competition, soil chemistry, nutrient cycling, near-ground microclimatic conditions, and community structure (Kielland et al., 2006).

Floodplains of major rivers on the North Slope are critical habitat for vertebrate herbivores, especially during winter when forage is limited to plants protruding from the snow (West and Meng, 1966; Kelsall, 1972; Mould, 1979; St-Georges et al., 1995). We sampled along a riparian transect extending 568 km from the northern Brooks Range to the Arctic Coast. This transect spanned major environmental gradients and ecoregions in Arctic Alaska, allowing us to assess shrub requirements for each herbivore. Specific objectives of this study were to (1) quantify habitat thresholds for the three herbivores, (2) test whether forage requirements explain herbivores' distributions, and (3) examine overlap in resource use to assess competition.

We tested the importance of forage requirements in explaining patterns of occurrence by moose, snowshoe hares, and ptarmigan at the northern edge of their distribution. If distributions are determined primarily by foraging needs, then we would expect small-bodied species to be widely distributed and large-bodied species that require more forage to be limited to areas with greater shrub biomass. Moose, the largest browsers among the target species, require approximately 70 times more forage biomass than snowshoe hares and nearly 200 times more than ptarmigan (Table 1). Thus, we expected ptarmigan to be most widely distributed, snowshoe hares to have an intermediate distribution, and moose to have the most restricted distribution.

Interspecific interactions, such as competition, can also influence species range-expansion dynamics (Sven-

TABLE 1

Body mass and daily energy requirements of each study species.

Species	Body weight	Source	Daily caloric intake	Source
	(kg)		(kcal/individual/day)	
Moose	750	[1]ADFG Titus et al. (2009)	21,211	Schwartz et al. (1988)
Snowshoe hare	1.6	ADFG Hart et al. (1965)	311	Hart et al. (1965)
Ptarmigan	0.6	ADFG [2]CLO	111	Mortensen and Blix (1989)

[1]ADFG, Alaska Department of Fish and Game; http://www.adfg.alaska.gov/index.cfm?adfg=animals.main
[2]CLO, Cornell Lab of Ornithology; http://www.birds.cornell.edu/

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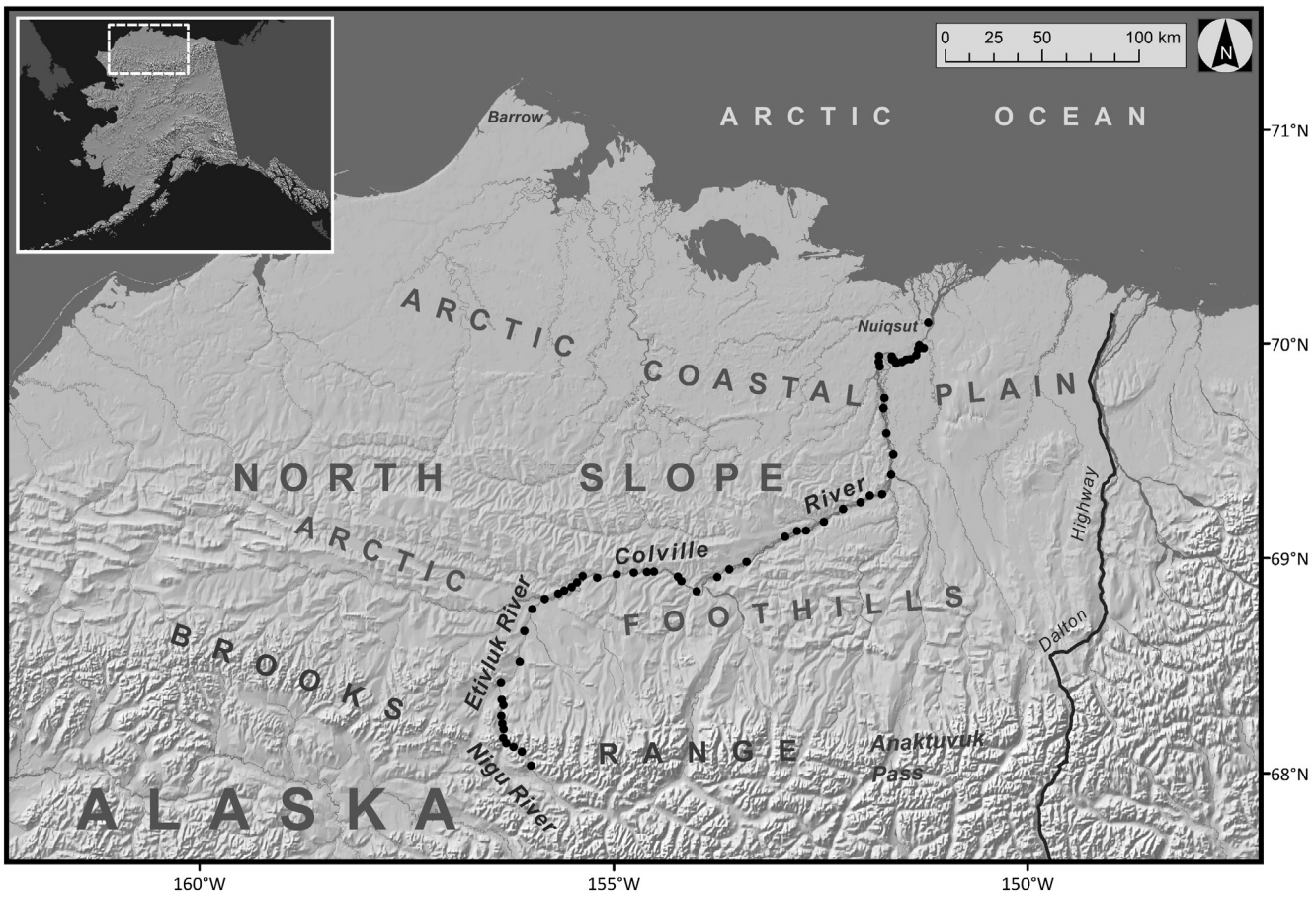


FIGURE 1. Shrub sampling sites (black dots) along floodplains of three rivers on the North Slope of Alaska.

ning et al., 2014). Without consideration of species interactions, the climate envelope per se is often not sufficient to predict species range shifts (Davis et al., 1998). Further, range shifts cause changes in community interactions and in most cases intensify competitive interactions (Tylianakis et al., 2008; Blois et al., 2013; Lancaster et al., 2017). With novel species migrating into the new habitat, we predicted a resource overlap between previously established species and new arrivals at the leading-edge communities. Therefore, we examined the potential for competition among the herbivores by examining overlap in use of different shrub species.

Methods

Study Area

The study area (Fig. 1) includes three physiographic regions on the North Slope of Alaska: the Brooks Range, Arctic Foothills, and Arctic Coastal Plain (68.16N, 156.04W to 70.22N, 150.89W). We selected riparian corridors along the Nigu, Etivluk, and Colville Rivers for sampling. The study area was selected because it spanned the northern expansion zone of shrubs and herbivores and exhibited variability in shrub characteristics.

The study region is an arctic tundra ecosystem dominated by tussocks and dwarf shrubs (e.g., *Salix reticulata*, *Betula nana*). Tall shrubs (>1 m), especially feltleaf willow (*Salix alaxensis*), occur commonly along creeks and river floodplains, where shrubs form strips of dense thickets that have expanded since 1950 (Tape et al., 2006; Naito and Cairns, 2011). The average annual temperature on the North Slope is –12 °C and July and February are the warmest and coldest months. Most of the average annual precipitation, about 250 mm, occurs during July and August (Huryn and Hobbie, 2012). The entire area is covered with snow up to eight months each year (October–April), and shrubs exceeding 0.5–1.0 m are usually the only vegetation visible between January and snowmelt.

Site Selection

From 11 August to 1 September 2014, we used inflatable boats to float down three connected rivers,

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where we randomly selected transect sites by generating random numbers for stopping times. At each stop, a 50 m transect perpendicular to the river was sampled. The transect was started with the first point that hit vegetation when walking perpendicularly from the river, and shrubs were sampled at five locations along the transect (at 10, 20, 30, 40, and 50 m). At each location, we examined four sampling points. Both sides of the river were sampled by alternating right and left sequentially. In total, 59 transect sites were randomly selected in the river floodplains and 1180 sampling points were examined. The mean distance between transect sites was 7105 m (range: 1269–23,613 m).

Sampling Method

We used the point-centered quarter method (Mitchell, 2010) to characterize shrubs. At each of the five locations on the 50 m transect, we recorded the nearest shrub in each quadrant to the center of the location point, as well as canopy diameter of the thicket (composed of multiple stems that separately form an independent stand), shrub height, shrub species, terrace type, and browsing by herbivores. Terrace type was visually examined at each of the five locations along the transect, where four categories were assigned: 1 = most active (flooded > 1 yr^{-1}); 2 = active (flooded 1 yr^{-1}); 3 = inactive (rarely flooded); 4 = abandoned (no longer flooded).

When selecting the nearest shrub, distance was measured from the location point on the transect line to the center of the shrub thicket. The nearest shrubs were recorded only within a 5 m radius from the central point of the quadrants. The tallest live branch of the thicket was measured for shrub height. Diameter of the shrub canopy cover was determined using measurements of maximum and minimum diameters across the thicket canopy cover, which were later averaged in our analysis.

At distances of 10 and 30 m along each transect, we used a digital caliper to record diameter of current annual growth for each of the selected shrubs. These measurements were used to derive estimates of current annual biomass production at each site. All measurements during the entire sampling were performed by the same person to minimize potential measurement bias.

Browsing Intensity

Browsing intensity was measured as the proportion of stems browsed on each shrub, which was quantified by counting the number of both browsed and unbrowsed twigs from the randomly selected stems. The three herbivore species each leave distinct browsing marks on the shrubs (Christie et al., 2014). Moose browsing can be easily recognized by the ragged broken tips of browsed twigs, whereas snowshoe hares leave a sharp diagonal cut of twigs. Ptarmigan primarily consume buds but also feed on tiny twigs. Browsing marks were used as an index of presence in this region because moose in winter almost exclusively use areas with tall shrubs (Mould, 1979), and snowshoe hares are likewise restricted to shrubs protruding from the snow (Tape et al., 2016a). Although our sampling effort was a snapshot in time, estimation of browsing intensity and corresponding presence-absence inferences included not only current year browsing but also older browsing marks (~3 years prior).

Statistical Analyses

To identify shrub characteristics and site covariates important for predicting browse intensity, we used Pearson correlations among mean browsing intensity by each browser and the shrub characteristics at each site. Current annual twig biomass production for each shrub species was estimated using the field measurement of twig diameter of current annual growth and the allometric equation relating diameter to twig biomass reported by Seaton et al. (2011) in Alaska:

$$\text{Twig dry biomass (g)} = e^{a} \times e^{mse/2} \times \text{diameter}^{b}, \qquad (1)$$

where e is the base of the natural logarithm, a is the intercept, b is the slope, and diameter is the measured live twig diameter (mm). Each shrub species has a different coefficient estimated by Seaton et al. (2011) for the above equation. Shrub canopy volume was calculated by using the volume formula for a cone, where shrub height was multiplied by canopy area (πr^2) and divided by 3 (Bryant and Kothmann, 1979).

To quantify selection at the individual shrub thicket level (i.e., local scale), we used a progressive resource selection function (RSF). RSF uses binary observations of presence-absence (used vs. unused), or presence-available resource units to assess habitat selection (Boyce et al., 2002; Johnson et al., 2006). To generate RSF models for each species, we used presence-absence data of herbivore browse marks at each individual thicket (n = 937) as the response variable and individual shrub height as the explanatory variable. We used a stochastic gradient boosting (SGB) classification algorithm (Friedman, 2002) in TreeNet from Salford Predictive Modeler (SPM 7.0; http://www.salford-systems.com), which has been used for analyses of habitat preferences and thresholds (e.g., Cai et al., 2014). All the models based on SGB algorithm in TreeNet were selected and evaluated using the receiver operating characteristic (Fawcett, 2006). TreeNet was set

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to build 250 trees to reach the optimal tree numbers for the final models. We used the partial dependence plot produced by TreeNet to evaluate resource selection, which shows the marginal effect of shrub height on herbivore habitat resource use probability: a positive partial dependence indicates positive selection or preference and a negative partial dependence shows avoidance. Habitat resource selection is identified at the point where the response line on the *y*-axis crosses the *x*-axis and becomes positive in value (Popp et al., 2007).

To identify minimum shrub height thresholds at the site level (i.e., landscape scale), logistic regression was used based on site occupancy data. The presence-absence of browsing by each herbivore species along the 50 m transect at the sampling sites ($n = 59$) was used as the response variable. The maximum height of shrubs sampled at each site was averaged and used as the explanatory variable. By using the estimated coefficients of intercept and slope obtained from the logistic model, we calculated the mean shrub height that corresponded to a 50% chance of the species being detected at the site. The threshold was given by back-transforming from the logit link to proportions (*sensu* Suorsa et al., 2005) using the equation

$$\text{Threshold} = \exp\left(\frac{-\text{intercept}}{\text{slope}}\right) \times \left(\frac{1}{0.5} - 1\right)^{\frac{-1}{\text{slope}}}, \quad (2)$$

where the intercept and slope are values obtained from the logistic regression model.

Because ptarmigan were present at all but three sites, we conducted Firth's bias-reduced logistic regression using the 'logistf' (version 1.21) package (Heinze et al., 2013) in program R (R development Core Team, version 3.1.3) to avoid issues of complete or quasi-complete separation. In addition to likelihood ratio tests to assess overall model fit, we calculated the pseudo-R^2, or pR^2, for the models:

$$pR^2 = \frac{\text{null deviance} - \text{residual deviance}}{\text{null deviance}}. \quad (3)$$

The pR^2 measures the deviance explained by the model and provides a goodness-of-fit estimate analogous to the R^2 statistic in the linear regression (Hagle and Mitchell, 1992).

To examine the potential for competition among ptarmigan, hares, and moose, we examined resource use overlap in two ways: (1) browsing of the same individual shrubs (i.e., whether different herbivore species were browsing the same or different individual shrubs), and (2) the composition of shrub species browsed by each herbivore species. We used a null model approach to test for significant partitioning of individual shrubs and diet overlap. First, we compared the observed number of individual shrubs browsed by more than one herbivore species with the number that would be expected if herbivores were selecting individual shrubs randomly. To do this, we calculated the total number of individual shrubs browsed by each species, and we randomly assigned browsing to individual shrubs within the total sample ($n = 937$ shrubs) using the "sample" function in program R. We then determined the proportion of shrubs that were "browsed" by each species alone and by multiple species, and we ran the simulation 10,000 times to generate the average expected number of individual shrubs that would have been browsed by multiple herbivores if shrubs were selected randomly, along with 95% confidence intervals. To measure overlap in herbivores' browsing of shrub species, we used the 'EcoSimR' package (Gotelli and Ellison, 2013) to estimate pairwise diet overlap using Pianka's index (Pianka, 1973). 'EcoSimR' compares the observed overlap to a null model based on 1000 replications of Pianka indices created from randomly reshuffled diets.

Results

Across all species, the average canopy diameter was 63 cm ($SE = 0.08$ cm, range = 10–534 cm), mean canopy cover was 0.8 ($SE = 0.02$ m^2, range = 0.01–22 m^2), average volume of shrub thickets was 0.5($SE = 0.002$ m^3, range = 0.001–21 m^3), and averaged maximum height of shrubs was 80 cm ($SE = 0.09$ cm, range = 10–456 cm).

The tallest recorded shrubs were feltleaf willows (456 cm), with 41 individuals above 300 cm (Table 2). Accounting for 46% of recorded shrubs, the feltleaf willow was also the most common species recorded in the sampling area.

Shrub Height and Browse

For all three herbivores, browsing intensity was more strongly correlated with shrub height than any other examined characteristics of shrubs and sites, increasing with shrub height for all herbivores (Table 3).

Shrub height was tallest near the midpoint of our north-south transect. Height of some shrubs in the Arctic Foothills on the Colville River exceeded 4 m, whereas most shrubs at the beginning and end of the transect were less than 1 m tall. We observed ptarmigan browsing from our first sampling site in Brooks Range all the way to the last sampling site close to the Arctic Ocean. In contrast, moose and snowshoe hare browsing intensity followed the shrub height distribution and was observed only at sites with tall shrubs (Fig. 2).

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TABLE 2

Summary table of shrub characteristics. Height refers to the tallest branch. Cover refers to the average canopy diameter of shrubs. CAG diameter is the diameter of current annual growth twigs on each shrub. The number of measurements (*n*) is indicated.

	Height (cm)				Cover (m^2)			CAG diameter (mm)		
Shrub species	Mean	*SE*	*Min*	*Max*	Mean	*SE*	*n*	Mean	*SE*	*n*
Salix alaxensis	121	5.0	10	456	1.5	0.14	432	2.9	0.03	1639
S. arbusculoides	103	7.5	15	246	0.5	0.09	56	1.6	0.05	159
S. glauca/niphochlada	75	3.2	9	274	0.4	0.05	216	1.4	0.03	576
S. pulchra	71	5.1	11	189	1.0	0.22	69	1.7	0.05	191
S. richardsonii	60	3.0	13	141	0.2	0.04	112	1.6	0.03	250
Alnus sp.	172	11.1	27	297	2.0	0.66	46	2.4	0.06	148
Betula nana	28	—	—	—	0.1	—	1	1.3	0.10	10

The average height of shrubs browsed by ptarmigan, snowshoe hare, and moose was 110 cm (*SE* = 3.2 cm), 159 cm (*SE* = 8.3 cm), and 206 cm (*SE* = 9.3 cm), respectively. The Kruskal-Wallis H test showed a statistically significant difference in the height of shrubs browsed by the three species (Chi-squared = 127.263, df = 2, *P*-value < 0.001). The distributions of shrub heights browsed by each herbivore were distinct. Although ptarmigan browsing occurred along the entire spectrum of shrub height, their browsing was mainly concentrated in the low shrub height region. Moose and snowshoe hare browsing was concentrated in the tall shrub zones, though snowshoe hare browsing was concentrated on intermediate shrubs, whereas moose browsed both intermediate and tall shrubs (Fig. 3).

Shrub Height Selection

The TreeNet model (area under curve [AUC]: learning/testing = 0.90/0.91) indicated that moose predominantly browsed shrubs taller than 80 cm (Fig. 4, part A), snowshoe hares predominantly browsed shrubs taller than 60 cm (AUC: learning/testing = 0.84/0.81), and ptarmigan predominantly browsed shrubs taller than 30 cm (AUC: learning/testing = 0.89/0.88).

Minimum Habitat Thresholds for Site Occupancy

The site-level logistic regression model showed that sites with a mean shrub height of 81 cm (95% CI: 65–96 cm) had a 50% chance of moose presence (Fig. 4, part B; pR^2 = 0.50; χ^2= 40.534, df = 1, *P*-value < 0.001). Snowshoe hares had a 50% probability of presence when the average shrub height was 87 cm (95% CI: 67–94 cm; pR^2 = 0.36; χ^2= 28.685, df = 1, *P*-value < 0.001). Ptarmigan browsing was detected at most of the transect sites (56 of 59 sites), resulting in wide confidence intervals despite good model fit (pR^2 = 0.72), because of quasi-complete separation of presence and absence data (Fig. 4, part B). Firth's bias-reduced logistic regression model showed that ptarmigan had a 50% chance of presence at sites with average shrub height of 3 cm (χ^2= 11.1902, df = 1, *P*-value < 0.001) without reliable confidence intervals (lower 95% CI = 0), indicating no threshold. Ptarmigan browsing was detected at all sites with shrubs, except one site where only one feltleaf willow (height = 109 cm) was recorded along the transect.

All short shrubs (<1 m) browsed by moose (*n* = 17) were at sites with tall shrubs present (Welch two sample *t*-test, *t* = –6.1437, df = 15, *P*-value < 0.001). Only three short shrubs browsed by snowshoe hares were at sites without tall shrubs; all other short shrubs browsed by hares (*n* = 46) were at sites with tall shrubs (Welch two sample *t*-test, *t* = –2.9585, df = 6.007, *P*-value = 0.025).

Competition for Same Individual Shrubs

Of the 937 shrubs examined, moose browsed 117 (12%), snowshoe hares browsed 146 (16%), and ptarmigan browsed 736 (79%) shrubs. If the occurrence of shrub individuals browsed by herbivore species was random, we would expect to observe only 18 (95% CI: 11–26) shrubs browsed by both moose and hares. Instead, 43 shrubs were browsed by both moose and hares (Table 4), indicating selection for the same individual shrubs and potential competition if resources are limiting. Likewise, more individual shrubs were browsed by both moose and ptarmigan than expected, whereas overlap in browsing by hares and ptarmigan did not differ from random (Table 4).

Competition for Shrub Species

Despite a possible difference in preference of shrub species (Appendix Table A1), the dominant shrub species

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TABLE 3

Pearson correlation between herbivore browsing intensity and shrub characteristics (n = 937 shrubs). Correlation values (r) and P-values are provided. Height is the maximum live shrub height. Cover is the mean area of canopy cover. Volume was calculated by multiplying height and canopy cover and dividing by three. "Saal %" is the frequency of *Salix alaxensis*, expressed as percentage of the species occurrence among the total number of species recorded at each site. The combined percentage of *S. alaxensis* and alder is expressed as "AlnusSaal %." "TwigBio" is the dry weight of twig current year growth, calculated based on the measured twig diameter and estimated allometeric coefficients. "TerraceType" is the description of terrace types at each five sampling points along the transect, where four categories were assigned: 1 = most active (flooded > 1/year); 2 = active (flooded 1/year); 3 = inactive (rarely flooded); 4 = abandoned (no longer flooded). Log () and Sqr () stand for logarithm and square root, which were used for data transformation.

	Sqr(Height)		Log(Cover)		Log(Volume)		Sqr(Saal%)		Sqr(AlnusSaal%)		Sqr(TwigBio)		TerraceType	
Browsing intensity	r	P-value	r	P-value	r	P-value	r	P-value	r	P-value	r	P-value	r	P-value
Log(Moose)	0.71	0.00	0.43	0.00	0.48	0.00	0.09	0.51	0.24	0.07	0.45	0.00	0.12	0.37
Log(Hare)	0.63	0.00	0.35	0.01	0.39	0.00	-0.04	0.75	0.17	0.20	0.32	0.01	0.39	0.00
Ptarmigan	0.40	0.00	0.37	0.00	0.36	0.01	0.16	0.24	0.08	0.53	0.31	0.02	0.14	0.30

in the browse composition of all herbivores was feltleaf willow. For moose, 67% of total browsed shrubs were feltleaf willow; it was also the most common shrub species browsed by snowshoe hares (45%) and ptarmigan (48%). Occurrence of all other shrub species was low compared to feltleaf willow. The combined contribution of the next dominant species (*S. glauca* and *S. niphochlada*) was less than 30% of each herbivore's browse composition. The observed Pianka's diet overlap index, ranging from 0 (no overlap) to 1 (complete overlap), was 0.94 among all three herbivores, significantly higher than expected based on the null model (expected = 0.41, P-value < 0.001). The pairwise Pianka's overlap indices for the three species ranged from 0.93 to 0.96 and were all significantly higher than expected (0.37–0.47, P-value = 0.003–0.023).

Discussion

Along a 568 km transect spanning major environmental gradients and ecoregions on the North Slope of Arctic Alaska, we assessed shrub requirements for vertebrate herbivores, tested whether the level of forage requirement controls herbivore distribution patterns, and examined resource overlap among the herbivores. Our results show that shrub height was a key habitat characteristic explaining the distribution of these vertebrate browsers. Habitat threshold for hare occurrence (≥87 cm) was similar to that for moose (≥81 cm), whereas ptarmigan distributions were nearly ubiquitous (≥3 cm). These findings indicate that forage requirement appears to be sufficient to describe distributions of moose and ptarmigan, but not be sufficient to determine distribution of snowshoe hares, based on their relative size and shrub habitat requirement. We also found that overlap in use of shrub species was nearly complete, indicating potential competition among the herbivores if resources become limited (Hardin, 1960).

Habitat Thresholds and Distributions of Vertebrate Herbivores

At landscape scale, we detected no threshold for ptarmigan and they had the broadest distribution, which appears to be determined primarily by forage requirement and may be relatively less constrained by predation. Conversely, snowshoe hares have much lower requirement of forage than moose, yet they exhibited similar geographic distributions along our sampling transect (Fig. 2). Moose and hares were both restricted by the requirement of tall shrubs, with browsing on short shrubs occurring almost exclusively in the presence of tall shrubs. Moreover, the requirement of tall shrubs for moose at the landscape scale was validated by using an independent data set from Alaska Department of Fish and Game's 19-year aerial survey (unpublished data),

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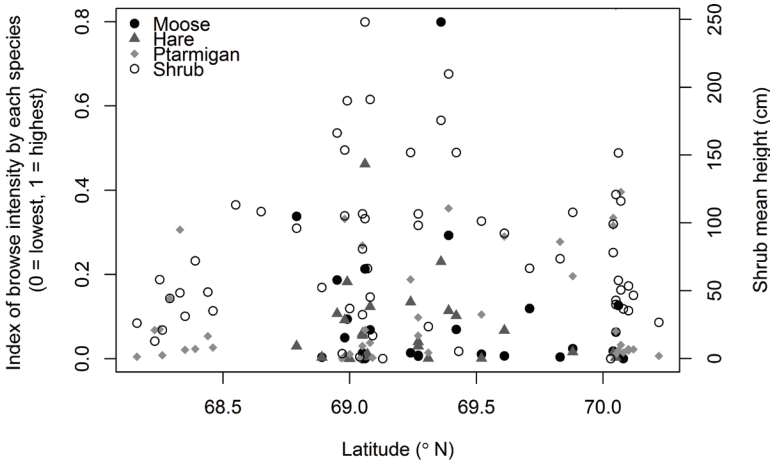


FIGURE 2. Herbivore species distributions and average shrub height (cm) are shown for each site along a north-south riparian transect on the North Slope of Alaska. Browse intensity levels (the proportion of stems browsed from each shrub thicket, from 0 to 100% removal of examined stems) of moose (filled circle) and snowshoe hare (dark triangle) followed the shrub height (open circle) distribution pattern in the study area, thriving along the tall shrub thickets of the middle Colville River but scarce in short shrub areas of the Brooks Range and Arctic Coastal Plain. In contrast, ptarmigan browsing (gray diamond) occurred across sites.

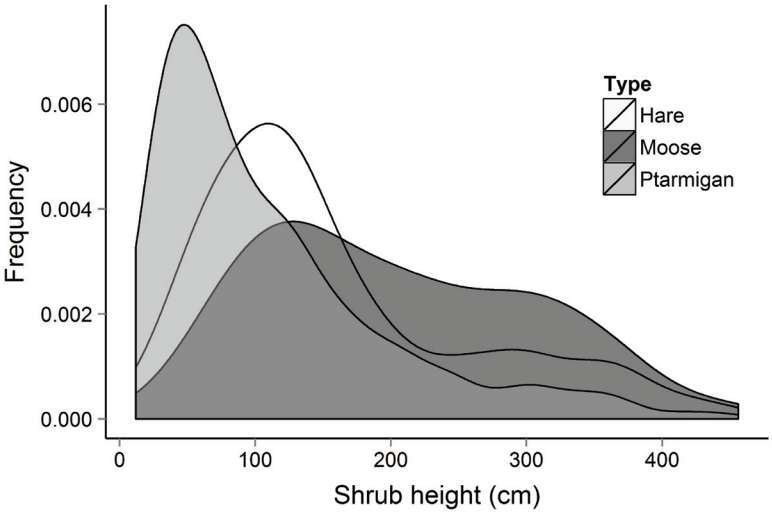


FIGURE 3. Height distributions of shrubs browsed by the three herbivores.

where most moose were in the floodplain areas with tall shrubs. In a section of Colville River within our study area, Mould (1979) also found that moose predominantly used riparian areas with tall shrubs. Tall shrubs in the riparian areas provide critical forage for herbivores in the Arctic. Our field measurements also showed that average shrub height at each sampling site was strongly correlated with average shrub volume ($r = 0.80$) and twig biomass production ($r = 0.58$), both of which can be considered as indices of forage biomass. Availability of forage during long arctic winters is essential to the survival and reproduction of herbivores like moose (Moen et al., 1997).

Based on snowshoe hare's small body size and caloric requirements compared to moose, we hypothesized a much smaller forage requirement than for moose; instead, snowshoe hares were found to have similar or slightly taller shrub habitat requirements than moose, indicating that tall shrubs also apparently function as cover for snowshoe hares. At the arctic tree line, Ewacha et al. (2014) suggested that snowshoe hares were more active in areas with greater canopy cover. Hares are vulnerable to predation (annual survival rate: 10–30%; Feierabend and Kielland, 2015) and rely on vegetative cover to avoid detection (Wolff, 1980; Wolfe et al., 1982; Litvaitis et al., 1985; Feierabend and Kielland, 2015). The spatial distribution and population cycling of prey species is influenced by predation risk (Korpimäki et al., 2004; Krebs, 2011), which may be a major control over the current distribution of herbivores such as snowshoe hares in this region. Previous studies indicated that availability of cover was more critical than food availability for forest-dwelling snowshoe hares (Bookhout, 1965a, 1965b; Buehler and Keith, 1982; Feierabend and Kielland, 2014), and that their distribution may be limited by predation (Sievert and Keith, 1985). Thus, the availability of tall shrub cover for predator avoidance may be the primary limiting factor in the northward range expansion of snowshoe hares in this region (Ewacha et al., 2014).

These findings further suggest that hares' habitat use at landscape level may be influenced by the "landscape of fear," a top-down effect imposed by perceived risk of predation (McNamara and Houston, 1992; Preisser et al., 2005). The use of landscapes by herbivores is often determined by the tradeoff between forage oppor-

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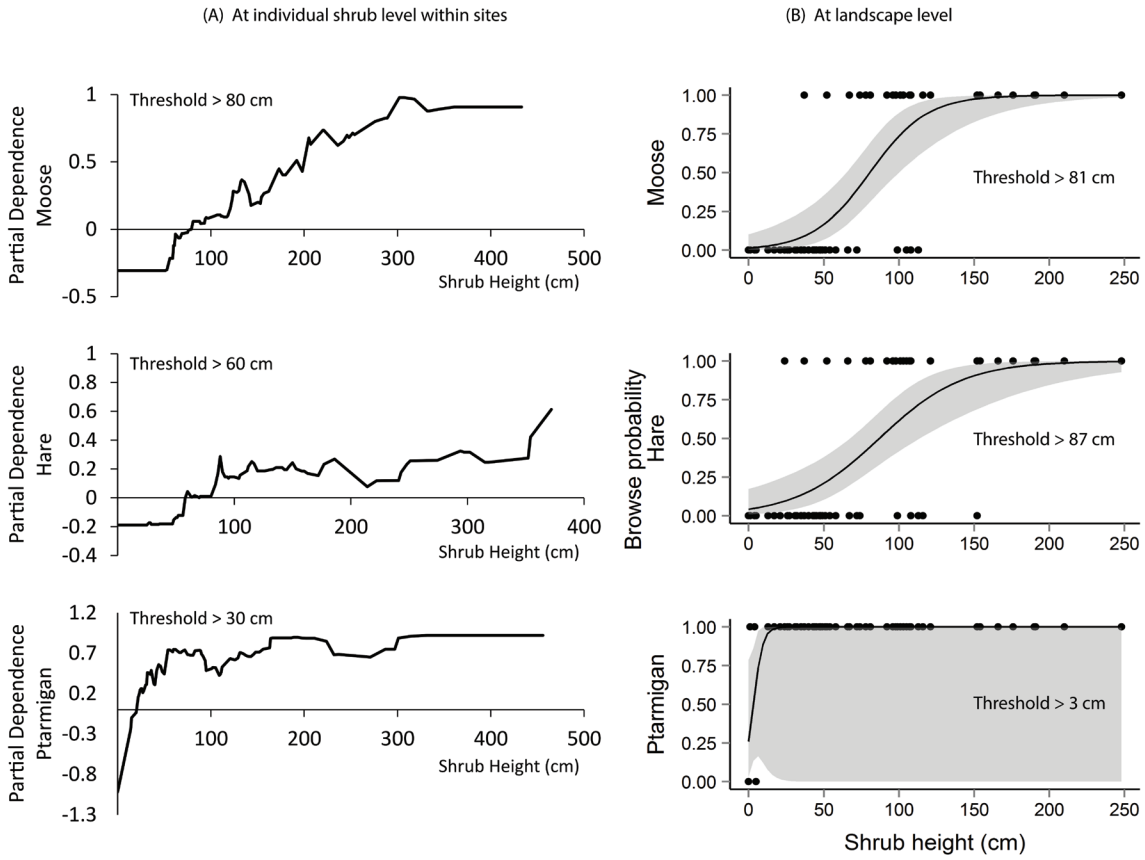


FIGURE 4. Habitat thresholds at individual shrub and landscape levels. (A) Partial dependence plots for habitat thresholds: moose, snowshoe hare, and ptarmigan. Positive partial dependence indicates resource preference by the species. Threshold is identified at the point where the response line on the *y*-axis crosses the *x*-axis and becomes positive in value. (B) Probabilities (solid line) of browsing by each herbivore along with 95% confidence intervals (gray band) in relation to mean shrub height at each sampling site.

TABLE 4

Overlap in use of individual shrubs by herbivores (*n* = 937 sampled shrubs). Observed numbers of shrubs browsed by each pair species are shown, as well as the expected number of shrubs based on random simulation with 95% confidence intervals.

Species pair	Observed	Expected (95% CI)
Moose and Hare	43	18 (11–26)
Moose and Ptarmigan	108	92 (84–100)
Ptarmigan and Hare	122	115 (105–123)

tunities and avoidance of predation risk (McArthur et al., 2014). For example, in an African savanna system in Kenya, Riginos and Race (2008) showed that herbivores, including zebras (*Equus burchelli*), hartebeest (*Alcelaphus buselaphus*), giraffes (*Giraffa camelopardalis*), and eland (*Taurotagus oryx*), preferred habitat areas with less predation risk. Our findings indicate that anti-predator behavior may thus play an important role in determining patterns of range shifts for some species responding to climate-induced changes to their habitat.

Within sampling sites, the resource selection thresholds (Fig. 4, part A) mirrored the order of body size and caloric intake requirements (Table 1). Moose preferred taller shrubs than snowshoe hares, and snowshoe hares preferred taller shrubs than ptarmigan. These results indicate there was resource partitioning in terms of shrub height among the vertebrate browsers within the sites at local scale, which may be due to the fact that browsers' body size determines their access to different shrub height (Dutoit, 1990). Because moose are much taller than hares (Table 1), they can easily access tall shrubs up to 2.5 m above the ground or snow surface (Borkowska and Konopko, 1994), whereas hares can only access taller shrubs in certain locations once accumulating snow provides a platform. Similarly, studies documented that ptarmigan predominantly browsed willow buds and twigs near the snow surface, concentrating below 1.5 m of willow height (Hakkarainen et al., 2007; Tape et al., 2010).

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Species Interactions and Resource Overlap

Species interactions can influence community composition changes and alter the course of response of ecosystems to climate change (Davis et al., 1998). We found that there was high overlap in resource use among the three herbivores, and was greatest between moose and snowshoe hares. The three vertebrate herbivores browsed similar species of shrubs. If shrub availability becomes limited, whether through the feedback of herbivory slowing down shrub expansion, increased consumption of preferred forage (Getzin et al., 2008; Post and Pedersen, 2008; Kaarlejärvi et al., 2015), or other environmental constraints (Naito and Cairns, 2011), our results indicate a potential for competition among the three species. An increase in snowshoe hare and ptarmigan abundance may reduce moose habitat quality (e.g. Bryant, 1987), and vice versa (e.g. Henden et al., 2011). However, because snowshoe hares have similar geographic distributions and habitat thresholds as moose, hares are likely to have a stronger impact on moose habitat quality than ptarmigan through competition (Belovsky, 1984). In the field, we often observed a hedge of short stems cut by hare browsing surrounding a few large stems standing in the thicket center that were too thick and tall for hares (Fig. 5); this browsing reduces forage availability for moose and ptarmigan, which can similarly control shrub architecture by browsing. Although shrubs respond to browsing by generating more branches to produce a "broomed" architecture, and possibly greater forage for herbivores like ptarmigan, heavy browsing by hares and moose can reduce shrub height and reproduction (Bryant, 1987; Butler et al., 2007; Christie et al., 2014).

Conclusions and Implications

Our results, in combination with climate projections, can help to predict future changes in shrub-dependent wildlife along their northern range limits. During the 20th century, shrub expansion facilitated the establishment of novel species like moose (Tape et al., 2016b) and probably snowshoe hares (Tape et al., 2016a) along major riparian shrub corridors throughout the Brooks Range and North Slope of Alaska. Here, taller shrubs were associated with more browsing by hares and moose, indicating that an increase in shrub height will increase the amount of available habitat for the two species. Due to their requirement for tall shrubs, however, the distribution of hares and moose in the Arctic will continue to be concentrated in shrub thickets following riparian corridors or other geomorphic disturbances.

In summary, we found that shrub height was the best predictor for occurrence of three herbivores and identified habitat thresholds for this guild of herbivores, which were previously lacking and will assist in developing models to identify and map suitable habitat for these herbivores based on shrub height distributions. We demonstrated that forage requirement alone will not determine the species distribution change for all shrub-dependent herbivores, an important consideration for

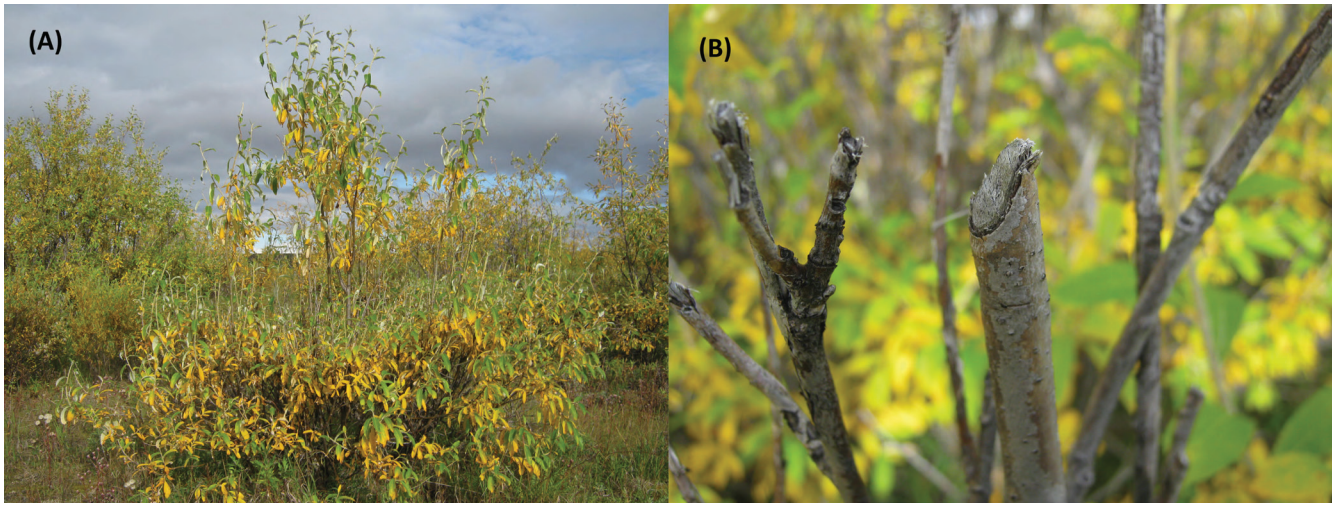


FIGURE 5. Snowshoe hare browsing impact on feltleaf willow. Browsing by hare has a pronounced impact on the shrub and may reduce forage availability for other herbivores like moose. (A) Impact of snowshoe hare browsing, where many short stems were evenly cut by hares, leaving a few unbrowsed tall standing stems at the center. (B) The diagonal cut of hare browse.

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future modeling of range expansion and ecosystem dynamics in response to global warming. The level of vulnerability to predation must be considered for some species. In addition, the high degree of potential interspecific competition for shrubs among the herbivores may substantially affect colonization dynamics of herbivore communities as the climate continues to warm in the Arctic.

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Appendix

TABLE A1

Preference indices table for moose (*Alces alces*), snowshoe hare (*Lepus americanus*), and ptarmigan (*Lagopus lagopus*, *L. muta*) in Arctic Alaska, where 1 = no preference, below 1 = avoidance, and above 1 = preference. Preference index was calculated as the ratio between browsed shrubs (i.e., percentage of each species in the browsed shrubs by the herbivores) and available shrubs (i.e., percentage of each species among the total number of shrubs recorded along the transect).

	Preference (use/available ratio)		
Species	Moose	Hare	Ptarmigan
Salix alaxensis	1.44	0.15	1.04
S. glauca/niphochlada	0.48	0.18	1.00
S. arbusculoides	1.14	0.36	0.86
S. richardsonii	0.43	0.08	1.22
Alnus sp.	2.08	0.24	0.63
Betula nana	0.00	0.00	0.00
S. pulchra	0.00	0.04	0.77

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