



BROWSE SELECTION BY MOOSE IN THE ADIRONDACK PARK, NEW YORK

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ABSTRACT: Moose (*Alces alces americana*), a large-bodied and cold-adapted forest herbivore, may be vulnerable to environmental change especially along their southern range in the northeastern United States. Better understanding of moose foraging patterns and resource constraints in this region, which moose recolonized over the past several decades, is needed to anticipate factors that may influence the long-term viability of the regional moose population. We quantified browse selection, intensity and nutritional quality, and the impact of other vegetation potentially interfering with browse availability for moose within the Adirondack Park, New York. We backtracked GPS-collared female moose (n = 23) to assess the seasonal composition of selected browse from 2016 to 2017, compared browse selection to plant nutritional quality, and modeled local browsing intensity. Moose demonstrated a generalist feeding strategy in summer, but in winter selected browse species largely in order of digestible dry matter. Red maple (*Acer rubrum*) was the most heavily used species in both seasons. Areas having a high proportion of beech (*Fagus grandifolia*), which in this region regenerates in dense thickets in the aftermath of beech bark disease and thwarts timber regeneration, were associated with reduced browsing intensity by moose in both seasons. Given the limited amount of timber harvest within the Adirondack Park, thoughtful management of harvested stands may increase marketable timber while also benefitting moose and ensuring the longevity of the New York population.

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Prior to European settlement, the geographic range of moose (*Alces alces americana*) in the northeastern United States extended south into northern Pennsylvania. During the 18th and 19th centuries, the range of moose receded northward as populations were decimated from unregulated harvests and given broad-scale conversion of forests to agricultural lands (Alexander 1993, Foster et al. 2002). Successful natural resource protection ultimately restored forest habitat for moose and recovered populations of native species such as beaver (*Castor canadensis*), whose maintenance of wetlands enhanced

habitat conditions for moose. By the mid-1980s, moose recolonized their eastern range as far south as northernmost Connecticut and the Adirondack Park in New York (Hicks 1986).

With a population of ~700 moose (J. Frair, unpubl. data), the 5.8 million-acre Adirondack Park and Forest Preserve in northern New York supports the lowest density of moose across comparable latitudes in their contemporary range in the Northeast (Wattles and DeStefano 2011). Following recolonization, New Hampshire and Vermont documented rapid growth in moose numbers

through the 1990s, with population stabilization observed through the mid-2000s, and more recently, declines in some areas. In contrast, the Adirondack moose population appears to have remained at low density since recolonization (Wattles and DeStefano 2011). Of the potentially limiting factors for moose within New York, the most influential are likely to include parasites (i.e., *Parelaphostrongylus tenuis* and *Fascioloides magna*) and limited abundance of quality food resources due to forest age. Although winter tick (*Dermacentor albipictus*) has been observed on moose in New York, the high levels of ticks infestation, tick-induced mortalities, and subsequent population declines observed in neighboring states has not yet been anecdotally documented likely owing to low moose density. Yet, in comparison to the larger populations in neighboring states, the Adirondack population is likely to be less resilient to changing environmental conditions given that numerical size is a key determinant in the viability of a population over time (Amos and Balmford 2001).

The forests inhabited by northeastern moose have experienced dramatic changes in canopy dominance due to invasive agents causing chestnut blight (early 1900s), Dutch elm disease (1920–1940s), and beech bark disease (1960s; Giencke et al. 2014). Shifts in canopy dominance precipitate cascading changes in the understory plant communities that, in turn, affect the herbivore community. Although moose successfully exploit non-traditional habitats in the Northeast, such as oak-dominated forests in Massachusetts (Wattles and DeStefano 2013), their behavioral plasticity to changing environmental conditions may be outpaced by that of white-tailed deer (*Odocoileus virginianus*; Post and Stenseth 1999). A high degree of behavioral plasticity in white-tailed deer has been evidenced by

their expansion into human-dominated landscapes (VerCauteren 2003), as well as northward expansion into the little disturbed boreal forests long considered primary moose habitat (Latham et al. 2011). Broad-scale overlap between moose and deer, especially along their southern range margin, poses concern for moose persistence owing to increased interspecies disease transmission and competition for resources.

Given differences in body size, morphology and energetic requirements, moose and deer have adopted differing foraging strategies (Irwin 1975, Ludewig and Bowyer 1985). Deer have relatively higher energy requirements than moose, and with their smaller muzzles can be selective for high energy and nutrient-rich plant parts. In contrast, moose are bulk feeders that require large bite sizes to meet their energetic needs, a feeding strategy that requires dense concentrations of browse. Landscapes that have a higher degree of heterogeneity may reduce spatial overlap, and therefore resource competition between moose and deer, by providing a multitude of foraging opportunities that meet their different foraging strategies. Across the northeastern states, the highest concentrations of browse, and by extension the highest densities of moose, occur on regenerating forests following timber harvest (Dunfey-Ball 2009), a cover type that remains relatively uncommon within the largely “Forever Wild” Adirondack forests. Where moose are concentrated within the Adirondack Park now and into the future, how many moose can be supported by the landscape, and the degree to which moose overlap white-tailed deer will be driven in large part by the structure and composition of suitable foraging habitat.

To assess moose foraging in the Adirondacks, we focused solely on browse because tree and shrub species compose

up to 90% of moose diets (Van Dyne et al. 1980, Belovsky 1981, Dungan and Wright 2005). We further focused on beech (*Fagus grandifolia*) as a potentially interfering species because in the aftermath of beech bark disease (Houston 1994), beech exhibits a “thicket” like growth form shown to suppress seedling survival by sugar maple (Hane 2003) and reduce floral species diversity (Giencke et al. 2014). Beech may be an important factor influencing available forage for moose due to its high abundance and large distribution within the region. Moreover, beech thickets form visually dense pockets of foliage potentially perceived wrongly by moose as suitable foraging habitat and costing them valuable foraging time. Lastly, we evaluated how much time moose spend browsing in foraging patches given the local abundance of both principle browse species and beech.

By identifying key forage considerations for moose, this work provides insights to habitat management for moose in the Adirondack region of New York. Current restraints on active resource extraction throughout large portions of the region limit the ability of wildlife managers and foresters to manipulate the landcover to meet environmental objectives. Therefore, our work can help inform management decisions in the limited areas where timber harvest is allowed. Herein, we sought to 1) investigate the seasonal composition of browse used by moose along their southern range boundary in the Adirondack Park and identify the principle species browsed by moose in the summer and winter, 2) quantify diet selection relative to plant nutritional quality and compare species-specific values of energy and digestible protein per season, and 3) model local browsing pressure as a function of the availability of desirable and potentially interfering woody species.

STUDY AREA

Established by the New York State Legislature in 1885, the Adirondack Park (Park) (43°57'08.9"N 74°16'57.5"W) encompasses ~5.8 million acres in northern New York consisting of both publicly (45%) and privately-managed land (49%; Fig. 1). The majority of public land is protected by Article XIV of the New York State Constitution as “forever wild forest,” which precludes resource extraction or development of any kind. In contrast, the majority of private land is designated for resource management and owned by timber companies that focus on harvest of white ash (*Fraxinus americana*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), red oak (*Quercus rubra*), black cherry (*Prunus serotina*), and white pine (*Pinus strobus*) (NYS DEC 2016). The forest community is a patchwork of the northern boreal ecosystem interspersed with temperate deciduous forests and large peatland complexes. Lower elevations with fertile soils support a diverse array of tree species dominated by American beech, yellow birch (*Betula allegheniensis*), paper birch (*B. papyrifera*), sugar maple, and red maple. Higher elevations are typically more coniferous, dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), white pine, and eastern hemlock (*Tsuga canadensis*) (Jenkins and Keal 2004). Elevations range from 30 m on the shores of Lake Champlain to over 1,600 m at the highest summit (Mount Marcy). Much of the Park consists of large glacial valleys that gradually rise in elevation to the High Peaks region in the east-central part. Average monthly winter temperatures range from -12 to -6°C, with summer monthly temperatures typically range from 20 to 26°C. Monthly precipitation averages 8–10 cm year-round (Jenkins and Keal 2004). Aerial surveys indicate 25 times more white-tailed deer than moose

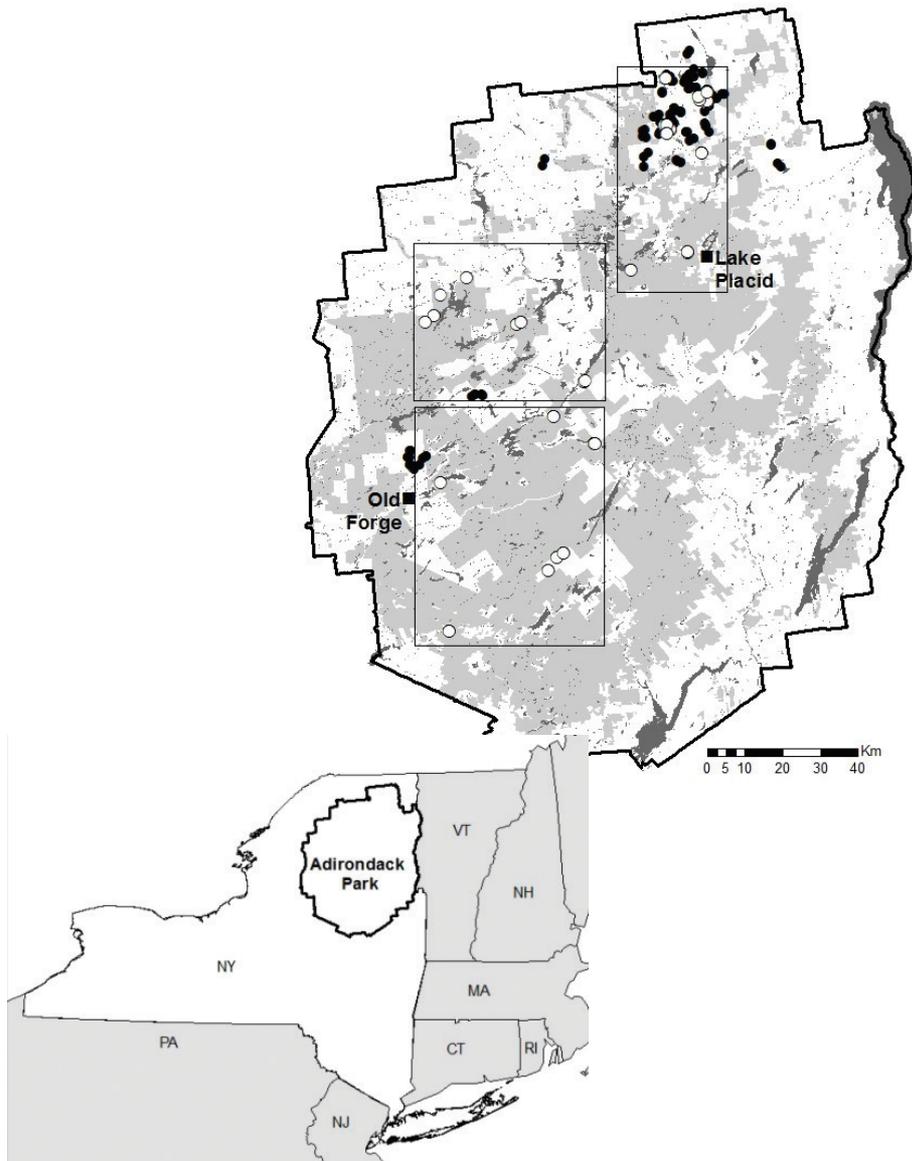


Fig. 1. Adirondack Park study area in northeastern New York, USA showing public lands (light gray) and private lands (white) along with water bodies (dark gray). Locations where GPS-moose were back-tracked are indicated (black circles) along with locations where nutritional samples were collected (white circles) and the grouping of nutritional samples (large boxes) to test for geographic variation in plant quality.

across the Park (J. Frair, unpubl. data). The region also supports sustainably harvested populations of two potential moose predators, black bear (*Ursus americanus*) and coyote (*Canis latrans*).

METHODS

Sampling Moose Browse

Adult female moose (n = 23) were captured in January 2015 to 2017, fitted with a GPS radio-collar (BASIC Iridium Track M 3D,

Lotek Wireless, Newmarket, ON or TGW-4670-3, Telonics, Mesa, AZ), and released on site (SUNY ESF IACUC protocol 140901). We programmed collars to attempt a GPS fix every 2 hours for 2 years, and collars achieved a mean fix rate of $98.7 \pm 1.1\%$. Following deployment, we back-tracked collared moose to quantify browsing patterns using procedures similar to Dungan et al. (2010), Seaton (2002), and Wilson (1971). We conducted summer sampling 15 Jun – 15 Jul 2016 and 2017, and winter sampling during the intervening Dec-Jan period. We concentrated search efforts on clusters of consecutive moose locations ($\sim 10\text{--}15$ GPS locations/ha) established by an individual over the previous 10-day window, and field visited clusters only after the animal had moved >500 m away. Two-three person field crews searched the vicinity of each GPS location cluster to record evidence of moose and deer. To avoid confusing browse by moose and deer, we did not sample areas for moose browse if deer scat or tracks were detected within 15 m of any portion of the subplots described below.

We defined the perimeter of the browsed patch following Bailey et al. (1996). Starting at a point central to the GPS location cluster, we walked in each cardinal direction until no browsed stems were observed on 5 consecutive individual trees or shrubs. Within that patch boundary, we established one transect having 3, 2- \times 4-m sub-plots spaced 10 m apart (Fig. 2). We defined browsable twigs as those <8 mm diameter that extended >15 cm from a given branch point to terminal bud, and that occurred within a 0.5–3 m height stratum (Crete and Jordan 1982, Raymond et al. 1996). We tallied the total number of browsed and unbrowsed twigs by species within each subplot. We measured basal diameter (10 cm above ground) or quantified volume (tallest height \times longest width \times perpendicular width) for each individual plant so

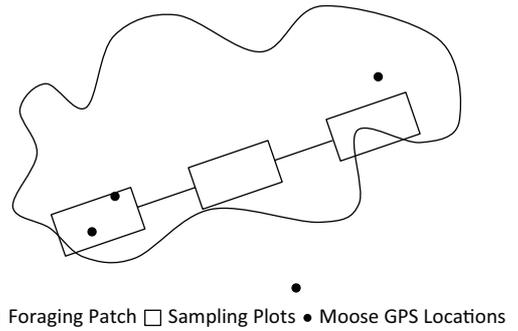


Fig. 2. Diagram of field sampling layout used to conduct browse selection surveys for moose in Adirondack Park, New York, USA. Sampling design consisted of three $4\text{ m} \times 2\text{ m}$ plots spaced 10 m apart on a transect. Plots were centered on an observed foraging patch that was located using GPS collared female moose. Edges of the foraging patch were delineated by walking concentric circles around an area of observed browse until no signs of moose browsing remained visible.

as to predict the total browsable biomass on that individual using allometric equations (Peterson 2018). We recorded the cover type of each transect as deciduous/mixed forest, conifer forest, open wetland, or wooded wetland based on classes derived from The Nature Conservancy’s Terrestrial Habitat Map for the Northeastern US and Atlantic Canada (Ferree and Anderson 2013) or, in forest management patches, as harvested stands ranging in cut age from 6 to 8 years (J. Santamour, LandVest, unpubl. data).

Browse Selectivity

We calculated proportional representation of each species, Pr_i , in the collective moose diet as:

$$Pr_i = \frac{T_i}{\sum_{i=1}^n T_i} \quad (1)$$

where T is the number of browsed twigs for each species i . In each season we ranked species in order by Pr_i and summed cumulatively across species. We assumed principle browse

species to be those, in rank order, whose cumulative proportional representation summed to 0.95. In the case where a principle browse species was geographically restricted (as described later), we substituted the next species in rank order until the 95% threshold was met to represent park-wide availability of principle browse for moose.

We summed the number of browsed and unbrowsed twigs on each transect to represent browse availability for species i , and we calculated two indices of selection for each species at the transect level. Ivlev's electivity index (Manly et al. 2002, Cook et al. 2016) ranges from -1 to $+1$ and was calculated as:

$$I_{ij} = \frac{\% \text{ Twigs Browsed} - \% \text{ Twigs Available}}{\% \text{ Twigs Browsed} + \% \text{ Twigs Available}} \quad (2)$$

for species i along transect j . Ivlev's index is symmetric about 0, facilitating direct interpretation of moose selection or avoidance of species i . In contrast, Chesson's index is bounded by 0 and 1, interpreted as the probability that the next bite will be of species i , and calculated as:

$$C_{ij} = \frac{\left(\frac{\text{Proportion twigs browsed}_i}{\text{Proportion twigs available}_i} \right)}{\left(\sum_{i=1}^n \frac{\text{Proportion twigs browsed}}{\text{Proportion twigs available}} \right)} \quad (3)$$

Nutritional Analysis

From principle browse species we collected 73 summer samples (Jul–Aug 2016, $n = 1-8$ per species, 29 locations) and 131 winter samples (Jan–Feb 2017, $n = 1-18$ per species, 37 locations), selecting individual plants to represent the size distribution measured during park-wide vegetation surveys (Peterson 2018). We clipped 5 browsable twigs (as previously defined) from various heights within the browse stratum per each sampled individual. We stored fresh clippings in plastic bags, kept them on ice in the field, and froze the samples as soon

as possible. Prior to nutritional analysis, we composited samples from different individuals by size class, with the included mass from a given size class proportional to the abundance of that size class across the landscape. We further organized composite samples to assess for potential variation in plant quality among central, northeastern, and southwestern portions of the Park. We analyzed replicate composite samples to quantify variation within a species and region (although not all species were sampled in all regions).

We sent frozen samples to the Wildlife Habitat and Nutrition Laboratory at Washington State University to determine crude protein (% CP), gross energy (cal/g, GE), neutral detergent fiber (% NDF), acid detergent fiber (% ADF), acid detergent lignin (% ADL), acid insoluble ash (% AIA), and bovine serum albumin protein precipitate (mg ppt./mg feed, BSA) (Goering and Van Soest 1970, Martin and Martin 1982, Robbins et al. 1987a). We used the BSA values to account for reductions in digestibility due to the tannin content of forage. Duplicate runs of NDF, ADF, ADL and AIA were conducted for each composite sample, with final values for analysis averaged across duplicates. Dry matter digestibility (% DMD) and digestible protein (g/100 g feed, DP) were calculated following Robbins et al. (1987a, 1987b). Digestible energy (kcal/g, DE) was determined as the product of GE and DMD for a given species. We used a one-way ANOVA to compare the mean values of DMD, DE, DP, CP, and BSA for species in which samples were available in multiple regions and Pearson's correlation coefficients to assess nutritional values for each species (DE, DP, DMD, CP, NDF, ADF, and BSA) and moose diet metrics (Pr_i , I_{ij} and C_{ij}) averaged across transects.

Modeling Browse Intensity

We used the number of stems browsed in plot k as a measure of local browse

intensity. We expected browse intensity at an individual plot to be influenced fundamentally by the availability of preferred browse within the larger patch. Total browsable biomass of all principle species on plot k (Bailey et al. 1996) was quantified using allometric equations (Peterson 2018), and summed across individual species along a given transect to provide a patch-level estimate. We modeled local browse intensity using standard and zero-inflated Poisson and negative binomial models using the R package `glmmADMB` (Bolker et al. 2012). The global model in each season included fixed effects for available browse biomass (linear and quadratic fits tested), proportion beech, proportion conifer, and two-way interactions among these three covariates. Models also included random intercepts for individual transect and moose. Covariates were centered and standardized prior to fitting models (Schielzeth 2010, Dormann et al. 2012). We compared alternative models using Akaike's Information Criterion with a bias adjustment for small sample size (AIC_c ; Burnham and Anderson 2002).

RESULTS

Principle Browse Species

We identified 13 and 12 principle browse species in summer and winter, respectively (Table 1, Appendix 1). Red maple constituted the largest portion of the diet in both seasons, representing 20.6 and 38.5% of the browse biomass consumed in summer and winter respectively. Yellow birch comprised 19.0% of the summer diet and 10.0% of the winter diet. Gray birch and paper birch made up 8.3 and 6.6% of the summer diet, respectively, but accounted for <1% each of the winter diet. In contrast, Balsam fir accounted for 16.5% of the winter diet, but was not detected in the summer diet. Though beech was abundant across the landscape, we found that it was rarely browsed by moose.

We included beech in our nutritional analysis due to the prevalence on the landscape and the potential for browse interference.

Selection Indices

For principle browse species, C ranged 0.04–0.39 with yellow birch and grey birch having the first and second highest C scores in summer, though their scores dropped precipitously in winter. Red maple ranked third according to C in summer but first in winter. According to values of I , in summer moose selected for striped maple, avoided sugar maple and hobblebush, and used the other species in proportion to their availability. In winter, moose selected for red maple while avoiding balsam fir, sugar maple, yellow birch, and black cherry. All other principle species were used in proportion to their availability. Among the non-principle browse species, winterberry (*Ilex verticillata*) was selected for in summer and willow (*Salix spp.*) in winter.

Nutritional Analysis

Northern wild raisin (*Viburnum nudum* L. var. *cassinoides*) and big-tooth aspen (*Populus grandidentata*) exhibited two of the highest DE values in summer at 2.85 and 2.76 kcal/g, respectively, concurrent with the two lowest DP values at 1.58 and 0.77 g/100 g feed, respectively. Low DP values are caused by relatively low CP content and, in the case of big-tooth aspen, compounded by a high reduction in digestion due to tannins (0.08 mg ppt/mg forage). Red maple, the largest component of moose diets in both seasons, exhibited moderate values for all nutrients measured. Perhaps the most nutritious forage in summer was pin cherry (*Prunus pensylvanica*), exhibiting the highest DP (6.20 g/100 g forage), and second highest DE (2.76 kcal/g) and DMD (55.24%; Fig. 3). Quaking aspen (*Populus tremuloides*; DE = 2.63 kcal/g,

Table 1. Browse metrics, including proportion of diet (*Pr*), Ivlev's Index (*I*), Chesson's Index (*C*), and Utilization (*U*) along with nutritional quality, including Digestible Energy (kcal/g, *DE*), Digestible Protein (g/100 g feed, *DP*) and Dry Matter Digestibility (% DMD), for principle browse species consumed by moose in summer and winter in 2016–2017 within the Adirondack Park, New York, USA. *N*₁ is the number of browse selection transects on which a given species was observed. *N*₂ is the number of nutritional samples collected for laboratory analysis of a certain species. Values in parentheses are standard deviations. For *I* and *C*, 95% confidence intervals that do not overlap 0 indicated by *.

Season	Principle Browse Species	Browse Metrics						Nutritional Quality			
		<i>N</i> ₁	<i>Pr</i>	<i>I</i>	<i>C</i>	<i>N</i> ₂	<i>DE</i>	<i>DP</i>	<i>DMD</i>		
Summer	<i>Acer pensylvanicum</i>	19	<0.01	+0.81(0.42)*	0.04(0.10)	8	2.62(0.15)	2.40(1.03)	53.65(3.21)		
	<i>Acer rubrum</i>	59	0.21	-0.06(0.63)	0.28(0.29)*	6	2.36(0.16)	2.24(0.80)	49.07(2.80)		
	<i>Acer saccharum</i>	23	0.05	-0.27(0.57)*	0.23(0.26)*	2	2.47(0.01)	2.79(0.10)	52.56(1.02)		
	<i>Acer spicatum</i>	3	<0.01	-0.06(0.83)	0.22(0.22)	-	-	-	-		
	<i>Betula alleghaniensis</i>	48	0.19	+0.11(0.52)	0.36(0.30)*	4	2.00(0.14)	3.12(1.12)	39.96(2.68)		
	<i>Betula papyrifera</i>	15	0.07	+0.05(0.66)	0.25(0.23)*	3	2.12(0.30)	3.68(0.82)	40.97(4.79)		
	<i>Betula populifolia</i>	11	0.08	+0.25(0.43)	0.33(0.27)*	7	2.23(0.21)	2.66(1.00)	43.13(3.87)		
	<i>Ostrya virginiana</i>	7	0.01	-0.37(0.80)	0.24(0.38)	-	-	-	-		
	<i>Populus grandidentata</i>	6	0.02	+0.30(0.45)	0.28(0.19)*	1	2.76(n.a.)	0.77(n.a.)	53.00(n.a.)		
	<i>Populus tremuloides</i>	13	0.05	-0.00(0.50)	0.20(0.13)*	-	-	-	-		
Winter	<i>Prunus pensylvanica</i>	13	0.06	-0.22(0.55)	0.22(0.30)*	3	2.76(0.12)	6.20(1.24)	55.25(2.38)		
	<i>Viburnum lantanoides</i>	17	0.02	-0.53(0.59)*	0.17(0.27)*	2	2.31(0.13)	3.30(0.54)	48.21(2.40)		
	<i>Viburnum nudum cassinoides</i>	18	0.09	-0.03(0.58)	0.23(0.19)*	5	2.85(0.21)	1.58(0.28)	56.15(4.04)		
	<i>Abies balsamea</i>	24	0.17	-0.31(0.50)*	0.22(0.30)*	18	2.68(0.20)	2.80(0.95)	49.60(3.54)		
	<i>Acer pensylvanicum</i>	20	0.06	-0.15(0.49)	0.18(0.21)*	5	2.18(0.09)	-0.35(0.24)	44.36(1.18)		
	<i>Acer rubrum</i>	38	0.39	+0.17(0.52)*	0.39(0.28)*	3	2.02(0.08)	0.19(0.46)	42.27(2.25)		
	<i>Acer saccharum</i>	14	0.01	-0.58(0.51)*	0.09(0.14)*	3	1.66(0.05)	0.37(0.44)	33.80(1.06)		
	<i>Acer spicatum</i>	5	0.01	-0.31(0.72)	0.22(0.30)	3	-	-	-		
	<i>Betula alleghaniensis</i>	17	0.10	-0.57(0.44)*	0.06(0.06)*	2	1.67(0.19)	2.89(1.91)	32.82(3.39)		
	<i>Populus grandidentata</i>	6	0.01	+0.09(0.63)	0.21(0.13)*	3	2.23(0.02)	2.61(0.52)	43.82(0.62)		
<i>Populus tremuloides</i>	11	0.03	+0.20(0.55)	0.31(0.27)*	4	2.63(0.15)	3.78(1.50)	50.85(2.74)			
<i>Prunus pensylvanica</i>	9	0.02	-0.40(0.63)	0.10(0.13)*	2	1.69(0.00)	0.96(0.91)	33.73(0.47)			
<i>Prunus serotina</i>	21	0.07	-0.54(0.50)*	0.10(0.15)*	1	1.85(n.a.)	3.23(n.a.)	34.76(n.a.)			
<i>Viburnum lantanoides</i>	17	0.03	-0.13(0.65)	0.22(0.26)*	3	2.17(0.09)	1.62(0.57)	45.27(1.15)			
<i>Viburnum sp.</i>	9	0.06	-0.01(0.46)	0.21(0.24)*	2	2.43(0.07)	0.34(0.06)	46.62(1.20)			

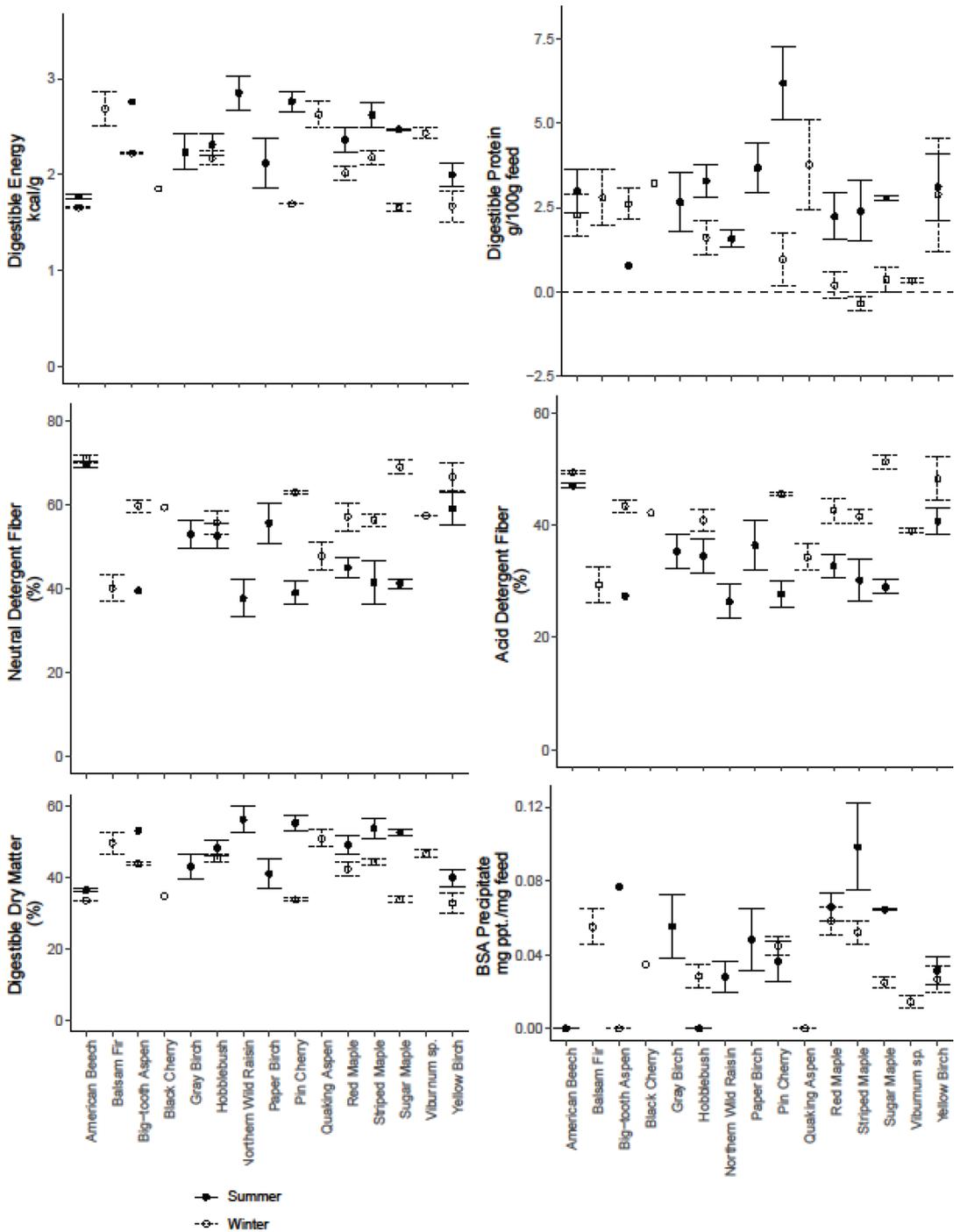


Fig. 3. Nutritional values, showing mean with 95% confidence interval, of principle browse species consumed by moose during the summer (Jun–Aug 2016; denoted by solid circle) and the winter (Dec–Feb 2017; denoted by outlined circle) in Adirondack Park, New York, USA. American beech, a potentially interfering browse type, is shown for comparison.

DP = 3.78 g/100 g feed, DMD = 50.85%, BSA=0.00) and balsam fir (DE = 2.68 kcal/g, DP = 2.80 g/100 g forage, DMD = 49.60%, BSA = 0.06 mg ppt/mg forage) were among the highest quality browse species in winter. For species collected in both seasons, DE, DP, and DMD were on average 18.65, 23.12 and 19.31% lower, respectively, across species in winter compared to summer. No regional differences in DMD, DE, DP, CP, or BSA were detected for any individual species (summer $p = 0.08-0.96$; winter $p = 0.15-0.98$). We found that striped maple had a DP value of less than 0 in winter, given the low average CP level (4.46%) was inhibited by the level of tannins (BSA = 0.052 mg ppt/mg forage).

American beech exhibited relatively low values for DE (1.77 kcal/g), DMD

(36.4%), and CP (7.40%) in summer. However, there was no observed reduction in digestibility due to tannins (BSA = 0.00) for this species resulting in a relatively large DP (3.00 g/100 g feed). In winter, American beech exhibited low DE (1.66 kcal/g) and DMD (33.60%) values with a moderate DP (2.30 g/100 g forage).

Both I and C were positively correlated with DE and DMD in winter ($0.62 < r < 0.76$, $p < 0.05$; Fig. 4). In contrast, nutritional metrics were not significantly related to diet metrics in summer ($-0.55 < r < 0.49$, $p > 0.05$).

Browse Utilization Models

Local browse intensity, as measured by the number of stems browsed on at plot, was best fitted in both seasons by a zero-inflated negative binomial model (α , the dispersion

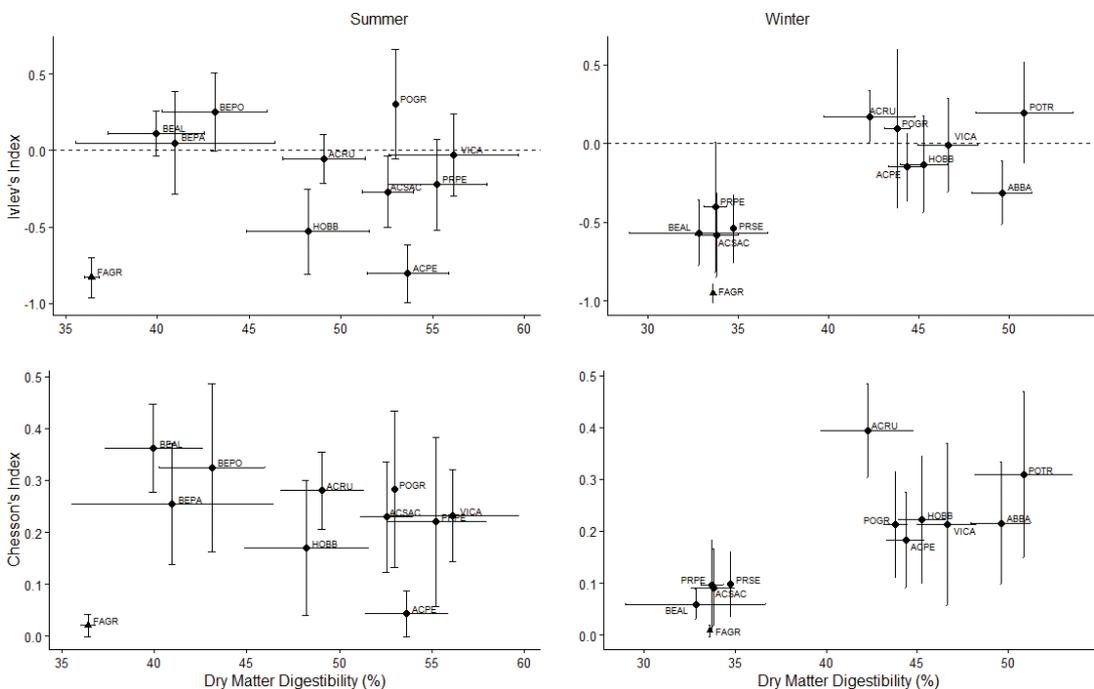


Fig. 4. Ivlev's Electivity Index (top panels) and Chesson's Index (bottom panels), with 95% confidence intervals, plotted as a function of Dry Matter Digestibility (DMD) in summer (left panels) and winter (right panels) for moose principle browse species and American Beech (FaGr; non-principle browse species) in 2016–2017, Adirondack Park, New York, USA. Species are labeled using the first two letters of their genus and species (see Table 2 for scientific names), beech plotted only for comparison and not used in statistical analyses.

parameter, for global models = 1.10 [SE = 0.16] in summer and 2.39 [SE = 0.88] in winter). In summer, model selection uncertainty (based on $\Delta\text{AIC} < 2.0$) involved interaction terms and whether total available browse was better fit with a linear or quadratic form (Table 2). The top ranked model in summer indicated the effect of total browse biomass on browse intensity saturated at $\sim 31,250$ kg/ha in the absence of other covariates (Fig. 5). However model selection uncertainty on the quadratic term suggests that browse intensity may be equally well represented by a linear function of increasing biomass availability. In winter, model selection uncertainty centered on the

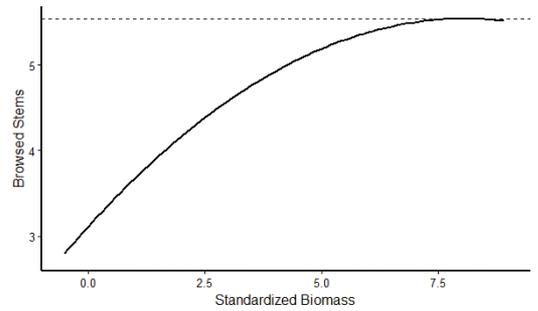


Fig. 5. Plot of browse intensity by moose in summer across the observed range of standardized browsable biomass values, holding beech and conifer coverage at a value of 0. Maximum browsing intensity is encountered at approximately 7.5 standardized biomass units (2.5 kg/m²; see Appendix 2 for standardization values), Adirondack Park, New York, USA.

Table 2. Comparison of top 10 candidate models (summer cumulative weight = 0.58, winter cumulative weight = 0.96) predicting local browse intensity by moose in 2016–2017 in the Adirondack Park, New York, USA as a function of the principle browse biomass (M; fitted as a linear or polynomial), proportion stems beech (B), proportion stems conifer (C), and interactions as indicated. For each model, the model degrees of freedom (df), estimated log-likelihood (LL), difference in AICc value (ΔAIC_c), and AIC model weight (w) are reported.

Season	Model	Main Effects	Interactions	df	LL	ΔAIC_c	w
Summer	1	M+M ² , B, C	MxB, MxC, BxC	12	-872.29	0.00	0.11
	2	M, B, C	MxB, BxC	10	-874.73	0.42	0.09
	3	M, B, C	MxB, MxC, BxC	11	-873.75	0.69	0.08
	4	M+M ² , B+B ² , C	MxC, BxC	12	-872.76	0.94	0.07
	5	M, B, C	MxC, BxC	10	-875.25	1.46	0.05
	6	M+M ² , B+B ² , C	BxC	11	-874.22	1.62	0.05
	7	M+M ² , B, C	MxC	10	-875.43	1.82	0.04
	8	M+M ² , B+B ² , C	MxB, BxC	12	-873.37	2.16	0.04
	9	M+M ² , B		8	-877.80	2.19	0.04
	10	M+M ² , B+B ² , C	MxB, MxC, BxC	13	-872.29	2.26	0.03
Winter	1	M+M ² , B		8	-578.66	0.00	0.35
	2	M+M ² , B, C		9	-578.14	1.27	0.19
	3	M+M ² , B	M×B	9	-578.58	2.14	0.12
	4	M+M ² , B, C	M×C	10	-578.09	3.50	0.06
	5	M+M ² , B, C	M×B	10	-578.11	3.55	0.06
	6	M+M ² , B, C	B×C	10	-578.14	3.61	0.06
	7	M+M ²		7	-581.70	3.81	0.05
	8	M+M ² , C		8	-581.08	4.84	0.03
	9	M+M ² , B, C	M×B, M×C	11	-578.08	5.87	0.02
	10	M+M ² , B, C	M×C, B×C	11	-578.09	5.88	0.02

inclusion of conifer as an interfering vegetation type. During winter, browse intensity was predicted to peak at ~4,200 kg/ha of principle browse. The amount of beech in the patch had a negative effect on browse intensity in both seasons, and conifer abundance had a negative effect on browse intensity in summer (Table 3).

The top summer model showed that undesirable woody plants (beech and conifer) negatively affected local browse

intensity by moose, an effect not observed in the winter. Although browsing intensity increased with total biomass of principle species, interactions showed a predicted reduction in browse intensity as the proportional coverage of beech or conifer increased. The impact of beech on browsing intensity was greatest at lower levels of browsable biomass and diminished with increasing biomass (Fig. 6A). In contrast, proportional coverage of conifer increasingly

Table 3. Standardized coefficient values for zero-inflated negative binomial regression models describing the local browse intensity (BI) by moose in the Adirondack Park, New York, USA given the amount of browsable biomass as well as potentially interfering species (beech and conifer). Data were standardized within a season prior to model fitting (see Appendix 2 for standardization values).

Covariate	Summer				Winter			
	β	SE	z	P	β	SE	z	P
Intercept	3.11	0.11	27.51	<0.01	3.67	0.13	27.39	<0.01
Browse Biomass	0.60	0.16	3.67	<0.01	0.71	0.17	4.14	<0.01
Browse Biomass ²	-0.04	0.02	-1.73	0.08	-0.14	0.04	-3.62	<0.01
Proportion stems beech	-0.95	0.22	-4.29	<0.01	-0.27	0.11	-2.48	0.01
Proportion stems conifer	-0.65	0.19	-3.45	<0.01	-	-	-	-
Biomass × Beech	0.22	0.24	0.92	0.36	-	-	-	-
Biomass × Conifer	-0.25	0.17	-1.46	0.14	-	-	-	-
Beech × Conifer	-1.06	0.39	-2.74	0.01	-	-	-	-

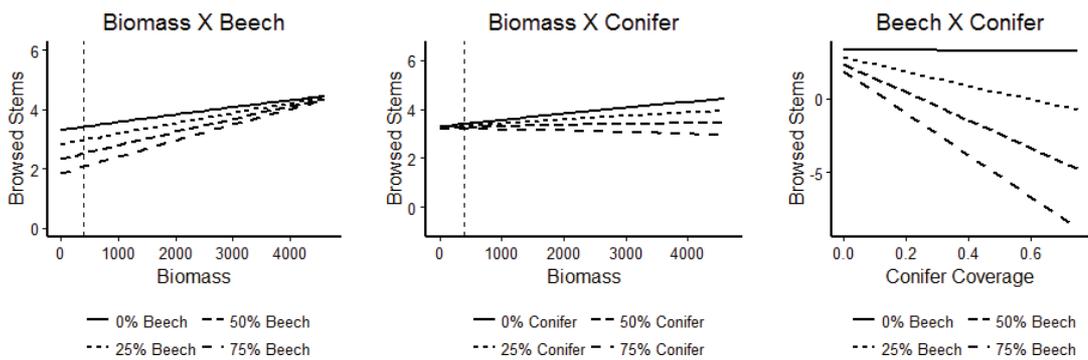


Fig. 6. Partial slope plots of biomass, conifer coverage and beech coverage interactions for models predicting browsing intensity (number of stems browsed) of moose during summer at a given location in Adirondack Park, New York, USA. Browsed stems are estimated at the plot (8 m²) level. Biomass values (x-axis, panels A and B) are shown in g/8 m² plot, and span the range of 95% of observed values of biomass (Peterson 2018). Levels of beech and conifer coverage are also restricted to 95% of observed values for each variable (~75% coverage for each). Vertical dashed lines represent average browse biomass estimated in regenerating forest (400 g/8 m², or 0.05 kg/ha).

diminished browsing intensity as total browsable biomass increased (Fig. 6B). Where occurring together, conifer and beech species had a compounding reduction on browse intensity (Fig. 6C).

DISCUSSION

Iconic of the north woods and wilderness areas, moose are a culturally as well as ecologically important species in the northeastern United States. Along their southern range in this region lies the Adirondack Park – the largest protected area within the contiguous United States. This study is the first to quantify moose diets and forage quality within the Park, establishing an important baseline for understanding potential climate-induced threats to moose habitat quality in the future. The composition of moose diets was similar to that observed in New Hampshire (Pruss and Pekins 1992) but quite different from that observed in Maine (Ludewig and Bowyer 1985). Red maple, pin cherry, and quaking aspen were used by New Hampshire and Adirondack moose alike, but speckled alder (*Alnus incana*), a commonly browsed species in New Hampshire, was not used, although widely available in wetlands. Winter diets in Maine were dominated by balsam fir (70.5%), American beech (11.4%), and hawthorn (*Crataegus* spp., 9.3%) (Ludewig and Bowyer 1985), versus red maple and balsam fir in the Adirondacks.

Generally, herbivore diet selection correlates with relative nutritional content (Hobbs and Swift 1985, Hanley 1997). Winter moose diets in the Adirondacks correlated positively with dry matter digestibility (and by extension digestible energy) and negatively with fiber concentrations. Balsam fir was one of the highest quality browse species in winter along with quaking aspen. Spatial variation in plant-nutritive quality was not observed across the vast Adirondack Park despite meaningful differences in terrain and

soil characteristics (Miller 1914) and the expectation that plant secondary compounds and other components can be spatially diverse within species (Gusewell and Koerselman 2002). Small sample sizes (summer: 1–2 samples/region, winter: 1–11 samples/region) may have precluded detection of differences among regions of the Park. However, our values for crude protein in balsam fir, striped maple, red maple, and hobblebush were 1–2% lower than previous studies elsewhere in the northeastern United States (Mautz et al. 1976, Raymond et al. 1996), potentially indicative of subtle regional differences but perhaps due to differences in laboratory techniques. The small degree of difference in our work compared to previous findings highlights that there is likely a limited difference in regional forage quality, allowing for comparisons in regional moose foraging work.

Although comparative studies in the northeastern US are lacking with respect to summer diet of moose, Renecker and Schwartz (1998) listed aspen, birch, and willow as species highly utilized across moose range. In our study, birch species comprised 34% of the summer diet of moose, aspen was relatively rare and generally utilized in proportion to its availability, and willow comprised <1% of the diet in each season. Generally speaking, moose were less selective in summer than winter, and patterns of browse selection did not reflect plant nutritional quality during summer. It is possible that moose base summer diet choices on nutrients or minerals not measured in this study, such as copper, sodium, or selenium (O'Hara et al. 2001, Custer et al. 2004). Moreover, moose make ready use of aquatic vegetation and herbaceous forage during summer, reducing their dependence on browse for meeting nutritional requirements.

Importantly, we observed that foraging decisions by moose, in particular local foraging intensity, may be influenced by the relative

abundance of undesirable species such as American beech that regenerates as shrub thickets as a legacy of beech bark disease. In both seasons, the proportional coverage of beech on a plot was associated with a reduction in local browse intensity. In summer, the difference in browsing intensity predicted between low and high biomass plots increased with increasing coverage of beech, notably by inordinately reducing browsing intensity in lower biomass plots. The interactive effect of beech on forage intensity was predicted to diminish towards zero with increasing amounts of browsable biomass; however, under average biomass conditions, foraging intensity was predicted to be ~12–41% lower in areas given ~25–75% beech coverage, respectively. Summer browse intensity was also predicted to decline as a function of proportional coverage of conifer species, although in contrast to beech, the relative impact of conifer increased within increasing browse biomass. Yet, at average biomass levels, little influence of conifer coverage is expected. Summer foraging sites with both high browse biomass and high conifer dominance (~50%) typically occur in canopy openings within mature conifer forest – those areas moose rely on for thermoregulation (van Beest et al. 2012), possibly explaining the expected reductions in forage intensity under these conditions in our study.

As moose are bulk feeders requiring large amounts of nutrients to maintain their large body size, effective use of their available foraging time is critical. Our work suggests that browsing intensity by moose is impacted directly by the availability of the biomass of principle browse species and indirectly by the amount of beech, and potentially conifer, relative to the total amount of browse. Maximum summer browsing intensity was predicted at approximately 2.5 kg/m², even under the highest value of beech coverage. Yet, managing forest stands to provide this

level of browse biomass to support moose is likely not feasible; on average, 0.05 kg/m² occurred in regenerating hardwood stands during summer (Peterson 2018). Under these average conditions, our models indicate that the value of forage to moose, as evidenced by moose foraging intensity, might be maximized by suppressing beech to <25% coverage.

The Adirondack Park in northern New York has a series of unique constraints that complicate managing forests and the fauna within. The government imposed “Forever Wild” status has ensured that the majority of mature forest in the region stays intact. However, small pockets of privately-owned forests can be harvested when enrolled in a state-sponsored easement program that includes state-mandated and approved management plans. As our work suggests, these private forests can provide ideal habitat for moose in that species that tend to thrive in timber openings due to their shade intolerance (*Acer* spp., *Betula* spp., and *Prunus* spp.) were preferred forage of Adirondack moose. Additionally, our work highlights the need for proactive steps to manage the composition of regenerating stands. Beech can often establish and out-compete more marketable tree species (e.g., *Acer* spp., *Prunus* spp.) following timber harvest, and by incorporating post-harvest stand management, managers can both increase their marketable yield and reduce the negative impacts of beech on moose browsing intensity. In so doing, forest managers may initially find increased browsing impacts by moose, although long-term impacts at higher moose densities are unsubstantiated in the northeastern United States (Bergeron et al. 2011, Andreozzi et al. 2014). Our findings are useful to wildlife managers working with private landowners to create management plans that can curate high quality moose habitat while mitigating issues associated with overbrowsing of commercially important species.

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APPENDICES

Appendix 1

Browse metrics for all species observed during moose browse selection surveys during summer (2016 and 2017) and winter (2016–2017) in Adirondack Park, New York, USA. The number of plots on which each species was observed is represented by N,

Chesson’s index values are represented by C, Ivlev’s electivity index values are represented by I, and the proportion of the total observed diet made up by each species is represented by Pr. Standard deviations for C and I are also displayed.

Season	Species	N	C	C (SD)	I	I (SD)	Pr
Summer	<i>Abies balsamea</i>	34	0.00	0.00	-1.00	0.00	0.00
Summer	<i>Acer pensylvanicum</i>	19	0.04	0.10	-0.81	0.42	0.00
Summer	<i>Acer rubrum</i>	59	0.28	0.29	-0.06	0.63	0.21
Summer	<i>Acer saccharum</i>	23	0.23	0.26	-0.27	0.57	0.05
Summer	<i>Acer spicatum</i>	3	0.22	0.22	-0.06	0.83	0.00
Summer	<i>Alnus incana</i>	7	0.00	0.00	-1.00	0.00	0.00
Summer	<i>Amelanchier</i> sp.	7	0.15	0.20	-0.36	0.81	0.01
Summer	<i>Betula alleghaniensis</i>	48	0.36	0.30	0.11	0.52	0.19
Summer	<i>Betula papyrifera</i>	15	0.25	0.23	0.05	0.66	0.07
Summer	<i>Betula populifolia</i>	11	0.33	0.27	0.25	0.43	0.08
Summer	<i>Caprinus caroliniana</i>	1	0.30	N/A	0.71	N/A	0.00
Summer	<i>Cornus</i> sp.	2	0.05	0.08	-0.55	0.64	0.00
Summer	<i>Corylus</i> sp.	3	0.40	0.27	0.39	0.38	0.00
Summer	<i>Fagus grandifolia</i>	37	0.02	0.07	-0.83	0.41	0.03
Summer	<i>Fraxinus americana</i>	7	0.05	0.09	-0.65	0.59	0.00
Summer	<i>Viburnum lantoides</i>	17	0.17	0.27	-0.53	0.59	0.02
Summer	<i>Ilex mucronata</i>	18	0.13	0.20	-0.42	0.64	0.06
Summer	<i>Ilex vericillata</i>	2	0.63	0.53	0.12	0.08	0.01
Summer	<i>Juglans cinerea</i>	1	0.00	N/A	-1.00	N/A	0.00
Summer	<i>Larix laricina</i>	4	0.00	0.00	-1.00	0.00	0.00
Summer	<i>Chamaedaphne calyculata</i>	3	0.00	0.00	-1.00	0.00	0.00
Summer	<i>Ostrya virginiana</i>	7	0.24	0.38	-0.36	0.80	0.01
Summer	<i>Picea rubens</i>	7	0.00	0.01	-0.91	0.23	0.00
Summer	<i>Pinus strobus</i>	1	0.00	N/A	-1.00	N/A	0.00
Summer	<i>Pinus sylvestris</i>	3	0.00	0.00	-1.00	0.00	0.00
Summer	<i>Populus grandidentata</i>	6	0.28	0.19	0.30	0.45	0.02
Summer	<i>Populus tremuloides</i>	13	0.20	0.13	0.00	0.50	0.05

Summer	<i>Prunus pensylvanica</i>	13	0.22	0.30	-0.22	0.55	0.06
Summer	<i>Prunus serotina</i>	19	0.13	0.17	-0.37	0.60	0.01
Summer	<i>Prunus virginiana</i>	8	0.05	0.09	-0.71	0.42	0.00
Summer	<i>Salix</i> sp.	5	0.17	0.15	-0.15	0.59	0.01
Summer	<i>Spiraea</i> sp.	4	0.00	0.00	-1.00	0.00	0.00
Summer	<i>Tsuga canadensis</i>	1	0.00	N/A	-1.00	N/A	0.00
Summer	<i>Vaccinium corymbosum</i>	3	0.00	0.00	-1.00	0.00	0.00
Summer	<i>Viburnum cassinoides</i>	18	0.23	0.19	-0.03	0.58	0.09
Summer	<i>Viburnum lentago</i>	2	0.16	0.19	0.02	0.67	0.00
Winter	<i>Abies balsamea</i>	24	0.22	0.29	-0.31	0.50	0.17
Winter	<i>Acer pensylvanicum</i>	20	0.18	0.21	-0.15	0.49	0.06
Winter	<i>Acer rubrum</i>	38	0.39	0.28	0.17	0.52	0.39
Winter	<i>Acer saccharum</i>	14	0.09	0.14	-0.58	0.51	0.01
Winter	<i>Acer spicatum</i>	5	0.22	0.30	-0.31	0.72	0.01
Winter	<i>Alnus incana</i>	2	0.06	0.05	-0.42	0.46	0.01
Winter	<i>Amelanchier</i> sp.	5	0.19	0.17	-0.02	0.59	0.00
Winter	<i>Betula alleghaniensis</i>	17	0.06	0.06	-0.57	0.44	0.10
Winter	<i>Betula papyrifera</i>	9	0.04	0.07	-0.67	0.50	0.01
Winter	<i>Betula populifolia</i>	4	0.07	0.12	-0.64	0.56	0.01
Winter	<i>Cornus</i> sp.	1	0.13	N/A	-0.05	N/A	0.00
Winter	<i>Corylus</i> sp.	1	0.00	N/A	-1.00	N/A	0.00
Winter	<i>Fagus grandifolia</i>	30	0.01	0.03	-0.95	0.16	0.01
Winter	<i>Fraxinus americana</i>	1	0.00	N/A	-1.00	N/A	0.00
Winter	<i>Viburnum lantoides</i>	17	0.22	0.26	-0.13	0.65	0.03
Winter	<i>Ilex mucronata</i>	3	0.13	0.07	-0.01	0.18	0.01
Winter	<i>Larix laricina</i>	1	0.00	N/A	-1.00	N/A	0.00
Winter	<i>Picea rubens</i>	13	0.02	0.09	-0.92	0.29	0.00
Winter	<i>Populus grandidentata</i>	6	0.21	0.13	0.09	0.63	0.01
Winter	<i>Populus tremuloides</i>	11	0.31	0.27	0.20	0.54	0.03
Winter	<i>Prunus pensylvanica</i>	9	0.10	0.13	-0.40	0.63	0.02
Winter	<i>Prunus serotina</i>	21	0.10	0.14	-0.54	0.50	0.07
Winter	<i>Prunus virginiana</i>	3	0.06	0.05	-0.46	0.47	0.00
Winter	<i>Salix</i> sp.	2	0.22	0.01	0.36	0.01	0.00
Winter	<i>Viburnum</i> sp.*	9	0.21	0.24	-0.01	0.46	0.06

Appendix 2

Standardization values used to center and standardize data for zero-inflated negative binomial regression to model browse utilization as a function of biomass availability, beech coverage, and conifer coverage, Adirondack Park, New York, USA.

	Summer		Winter	
	Mean	Standard Deviation	Mean	Standard Deviation
Principle Browse Biomass (g/8 m ²)	1288.776	2476.36	640.4	898.61
Beech Coverage	0.107	0.23	0.086	0.17
Conifer Coverage	0.143	0.245	0.136	0.252