



FORAGE AND HABITAT LIMITATIONS FOR MOOSE IN THE ADIRONDACK PARK, NEW YORK

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ABSTRACT: We used browse availability models to estimate the number of reproductive female moose (*Alces alces*) that could be supported during summer and winter in the predominantly forested 23,000 km² Adirondack Park and Forest Preserve (Park) in northern New York State, USA. We developed allometric equations to predict available browse biomass for individual plants and subsequent biomass estimates in 6 major cover types to estimate the moose carrying capacity within the Park. Our model incorporated the differential availability and nutritional quality of woody browse species within each cover type and changes in local browsing intensity due to competing vegetation under two different foraging constraints – protein and digestible energy. We estimated the carrying capacity as 8 (protein constraint) and 135 × (energy constraint) greater in winter than summer. Spatially-explicit estimates of summer range capacity (Animal Use Days, AUD) based on the protein constraint correlated best with variation in local moose density derived from winter aerial surveys ($R^2 = 0.75$, $P < 0.01$, $n = 18$). Protein availability was limiting in summer (AUD = 457 moose) with sparse patches of regenerating forest (< 20 years old) on privately-managed lands estimated to support 86% more moose than the dominant matrix of wetlands and mature mixed-deciduous forest. The small and patchy moose population in the Park reflects the relative scarcity of regenerating forest and optimal foraging habitat. Given statutory constraints of timber harvest in the majority of the Park, active forest management on private inholdings will play an outsized role in managing the moose population.

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The northeastern United States has one of the largest regional populations of moose (*Alces alces americana*) in North America (Jensen et al. 2018). However, within that region are pockets of low density moose as in the Adirondack Park and Forest Preserve in New York State that essentially represent the entire state population with density estimated as 0.03 moose/km² (J. Hinton, SUNY College of Environmental Science and Forestry, unpublished data). In contrast,

density in adjacent Maine, New Hampshire, and Vermont has been ≥ 0.3 moose/km² in recent decades (Wattles and DeStefano 2011). Unlike in nearby states, moose in the Reserve have limited access to large-scale anthropogenic forest disturbance associated with timber harvesting (Hicks 1986).

Moose require an abundance and dense concentration of quality woody browse to meet their nutritional requirements (Illius and Gordon 1987, Shipley et al. 1994),

and large-scale disturbances (fire historically) that set back forest succession creates optimal foraging habitat for about 20 years (Peek 2007). In the northeastern United States, the natural, large-scale return interval of inland forests is 1000–7500 years, and more often involves localized winter damage (e.g., ice storms) in small patches rather than large swaths of blown-down trees (Lorimer and White 2003, Millward and Kraft 2004). Small scale canopy disturbances from pathogens (e.g., hemlock woolly adelgid [*Adelges tsugae*]) and storms (i.e., winter blowdown) drive localized gap dynamics in the region (Runkle 1982, Seymour et al. 2002) producing diffuse patches of early seral vegetation. The local scale of these natural disturbances contrast with the more temporally and spatially predictable disturbances arising from timber harvest operations in the contiguous commercial forests of Maine, New Hampshire, and Vermont.

The geographic and population expansion of New England moose in the 1970–1990s was associated with unprecedented clear-cutting in response to a regional spruce budworm (*Choristoneura fumiferana*) infestation that created a contiguous swath of regenerating forest/optimal foraging habitat (Bontaites and Gustafson 1993, Wattles and DeStefano 2011); moderate-high populations have been maintained through continual timber harvest (Dunfey-Ball 2019). Research points to moose use and preference of regenerating forest habitat and early successional browse year-round throughout this area (Thompson et al. 1995, Scarpitti et al. 2005, Bergeron et al. 2011, Millette et al. 2014).

Understanding the relationship between availability and nutritional quality of forage resources is imperative to accurately assess the nutritional capacity of a landscape. Hobbs and Swift (1985) estimated the amount of

food required to achieve a diet of specific quality (i.e., food supply), which, when divided by daily dry matter intake rates for the target animal, provides an estimate of Animal Use Days (AUD). They used this approach in Colorado to evaluate differences in habitat quality between burned and unburned forests for bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) in comparison to traditional range supply models (Hobbs and Swift 1985). Hanley et al. (2012) expanded the AUD approach with their Forage Resource Evaluation System for Habitat (FRESH) with Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) by using a linear-programming model to estimate the maximum amount of forage biomass that could be pooled from available forage types, while meeting specified nutritional requirements under specific constraints including foraging time, bite size, and diet composition.

Importantly, such estimates only provide a “snapshot” carrying capacity of a given range. By assuming all available forage was harvested from a given area at a given point in time, the model approximates the days a captive animal is maintained at a desired nutritional plane. Such instantaneous estimates ignore plant-herbivore interactions, plant phenology, and dynamic metabolic requirements. As such, they are best interpreted as an index of habitat quality and for comparing the quality of different forage types, cover types, treatments, or areas at a given point in time (Cook et al. 2016). Though current models are best used as indices, incorporating additional constraints such as resource competition among forage species and accounting for uncertainty may yield estimates more realistic of field conditions (i.e., a multiplier effect; White 1983).

One often ignored aspect of estimating range quality is the compounding of

uncertainty as estimates of available biomass are scaled up from individual plants to local plot or transect measures, and again to the level of specific cover types or study areas. Dismissal of this attribute of sampling range quality can lead to biased or overly confident estimates of differences in range capacity across heterogeneous landscapes. Precision may be grossly overestimated when considered at a single foraging level only, as when accounting for inter-plot variation in biomass while ignoring the precision associated with allometric predictions of the biomass available on a given plant (McWilliam et al. 1993). Monte Carlo (MC) simulations can provide a useful approach to account for error propagation across multiple scales or processes (Harmon et al. 2007), and have been successfully used to estimate CO₂ uptake in pine forests (Bowler et al. 2012), carbon pools in subtropical forests (Conti et al. 2014), and nitrogen density in northeastern hardwood forests (Yanai et al. 2010).

We applied Monte Carlo simulations to 1) scale-up estimates of available browse biomass for moose from individual plants to major cover types, and 2) estimated range capacity for moose that accounted for uncertainty in forage quality and foraging constraints during summer and winter. Our approach identified the extent to which each component, whether measured empirically in this study or drawn from the literature, contributed to potential bias in and variance around range capacity estimates. We focused on digestible energy and protein as the two most limiting nutritional factors (Moen 1995). Ultimately, we compared the value of different plants and cover types to identify potentially limiting factors of habitat and management of moose within the Adirondack Park and Forest Preserve.

STUDY AREA

The study area was delineated as the 23,500 km² Adirondack Park and Forest Preserve of New York State, hereafter referred to as “Park” (43°57′08.9″N 74°16′57.5″W), of which ~45% is publicly-managed forest preserves interspersed with private inholdings (~55% of the landscape). The majority of public land is protected by Article XIV of the New York State Constitution as “Forever Wild” which precludes resource extraction or development of any kind. Approximately 25% of privately owned lands are designated for resource management including timber harvest through state-regulated conservation easements. Forest canopies in the region are dominated by American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), yellow birch (*Betula alleghaniensis*), and paper birch (*B. papyrifera*). Common conifer species include white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and balsam fir (*Abies balsamea*). Elevation in the Park ranges from <50 m on the shore of Lake Champlain to >1600 m in the High Peaks (Lake Placid) area. During data collection, monthly precipitation averaged 84.6 mm in May–September 2016, 84.2 mm in December 2016 – March 2017, and 128.3 mm in May–September 2017 (n = 17 weather stations; NOAA National Centers for Environmental Information).

METHODS

Plant Sampling

We sampled woody species along stratified transects (n = 104; Fig. 1) proportional to the coverage of upland mixed forest (≥ 497 m elevation, n = 38), lowland mixed forest (< 497 m, n = 34), conifer forest (n = 13), and wetlands (n = 19) within the Park using the generalized classification of the Terrestrial Habitat Map produced by The Nature

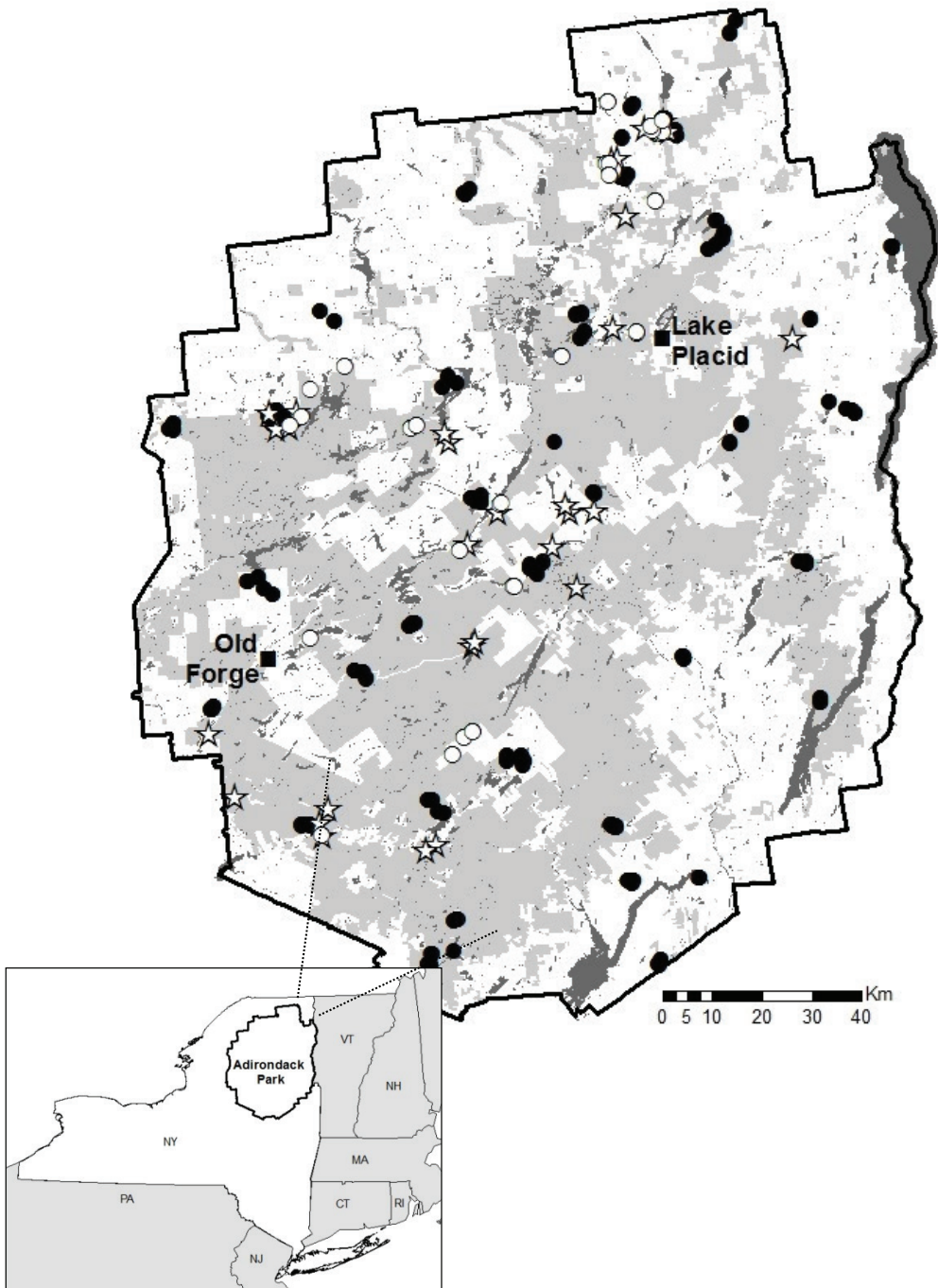


Fig. 1. Study area in northeastern New York State showing public lands (light gray; Wild Forest, Wilderness, Primitive Use and Canoe Areas), private lands (white; Rural, Low, Moderate, Industrial and Intensive Use, Hamlets and Resource Management Areas), and water bodies (dark gray). Also indicated are locations where browse biomass was sampled to build allometric equations (stars), transects where browse components were measured in the field and biomass was predicted using allometric equations (black circles), and locations where browse nutritional samples were collected (white circles).

Conservancy for the Northeast US and Atlantic Canada (Ferree and Anderson 2013; Appendix 1). We sub-stratified wetland transects into open wetland ($n = 15$) and forested wetland ($n = 4$) classes to capture vegetation patterns based on presence of mature trees within a given wetland. We placed 13 additional transects in the Chateaugay Woodlands area in the northern region of the Park to capture timber harvests of known age (6–8 years old; unpublished data, J. Santamour, LandVest Inc.). Transect start points were random locations (Create Random points in ArcGIS v.10.4) within each cover type; three 2×4 -m plots were spaced 50 m apart along a transect. To ensure that we adequately sampled the compositional and productive variation within a landcover type, random locations were spaced a minimum of 500 m from neighboring points. The direction of each transect was randomized using a random number generator (1–360) and modified as needed to ensure all sample plots fell within the same cover type. If we were unable to sample the same cover type within a given plot, we used another random point.

We collected summer samples in August–September 2016 and 2017 to assess peak biomass, and winter samples in December 2016 – January 2017. Individual plants were sampled to represent the full range of size observed along the transects (Peterson et al. 2020). We measured the basal diameter of the main stem (10 cm above the substrate) for tree growth, and the tallest height, longest width, and perpendicular width (to calculate volume) for shrub growth per individual plant (Peterson et al. 2020). We clipped all twigs that fell within a 0.5–3.0 m height stratum to 8-mm diameter, a cutoff expected to provide a liberal estimate of available biomass for moose by including both saplings and mature trees with biomass within the stratum (Seaton et al. 2002). Clippings collected in summer

included leaves and twigs, and winter clippings included twigs only for deciduous species and twigs plus needles for balsam fir. We separated and dried leaves and woody mass to a constant mass in a forced air oven at 90 °C for 24 h and weighed dried biomass to the nearest gram.

Allometric Equations

We developed allometric equations for the 14 species that comprised $\geq 95\%$ of the woody diet in winter and summer within the Adirondack region to more efficiently quantify available moose browse (McInnes et al. 1992, Visscher et al. 2006, Peterson et al. 2020). We developed a series of candidate models to evaluate environmental and topographical impacts on dried biomass per species. The dried mass (g) of each individual clipping was \ln -transformed to reduce the spread of error and to achieve a normally distributed error structure. We included the environmental site covariates of canopy cover, elevation, percent slope, and aspect. We calculated canopy cover as the average proportion of overstory covering a sample plot from 4 measurements at each of the cardinal directions with a convex densiometer. Elevation, percent slope, and aspect were derived from a 90-m resolution Digital Elevation Model (US Geological Survey) using ArcGIS (ESRI, Redlands, California, USA). Aspect was represented as a binary covariate with northwest values (0–40 degrees and 221–359 degrees) assigned as 0 and southeast values (41–220 degrees) as 1; southeastern facing slopes represent optimal plant growth conditions and increased species richness (Olivero and Hix 1998).

After initial inspection of the relationship between stem size and biomass, we collapsed species (and size classes within species) into 11 groups prior to fitting the final models rather than analyzing the models per individual species based on

taxonomic similarities (Peterson et al. 2020; Table 1). All groups were analyzed for the summer and winter seasons except balsam fir which moose consume in winter and avoid in summer (Peterson et al. 2020).

We evaluated candidate biomass models using all possible subsets with stepwise regression (Whittingham et al. 2006) and used Akaike's Information Criterion (AIC_c) for final model selection (Burnham and Anderson 1998). All model covariates were centered by the mean and standardized prior

to model fitting using a z-transformation (Schielzeth 2010). We calculated Pearson's correlation coefficient for our predictors and developed candidate models with all plausible covariate pairs having $r < 0.7$ (Dormann et al. 2012), as well as interactions between size and environmental site covariates. Additionally, we included quadratic covariates for basal diameter and volume to account for parabolic relationships in plant growth. In the case of uncertainty (i.e., where $\Delta AIC_c < 2.0$), we predicted biomass with the

Table 1. Allometric models predicting the browsable biomass available to moose in two consecutive winter and summer, 2016–17 as a function of \ln basal diameter (BD; for tree species only), volume (V; for bush species only), percent canopy cover (C), elevation in m (E), percent slope (S), and aspect (A). N indicates the number of samples within each group. Interactions among covariates are indicated by “:”.

Group	Species included	N	Season	Model	Adj. R ²
Balsam fir	<i>Abies balsamea</i>	17	Winter	+8.39 + 0.88BD – 0.01E + 1.04A	0.88
Maples Sm ^a	<i>Acer rubrum</i> , <i>A. saccharum</i>	15	Summer	–2.09 + 2.05BD	0.62
			Winter	–1.43 + 1.89BD – 0.13S	0.71
Maples Lg ^b	<i>A. rubrum</i> , <i>A. saccharum</i>	17	Summer	+14.53 – 0.02E	0.29
			Winter	+14.92 – 0.02E	0.32
Maples 3	<i>A. pennsylvanicum</i> , <i>A. spicatum</i>	16	Summer	–8.25 + 6.75BD – 0.85BD ² – 3.51A + 0.31(BD ² :A)	0.88
			Winter	–0.01 + 1.17BD – 13.79A + 4.12(BD:A)	0.85
Birches	<i>Betula populifolia</i> , <i>B. papyrifera</i> , <i>B. alleghaniensis</i> , <i>Ostrya virginiana</i>	27	Summer	+0.7 + 3.66BD – 0.52BD ² – 0.02C – 0.79S + 0.17(BD:S)	0.84
			Winter	–26.44 + 15.49BD – 1.85 BD ² + 0.2C – 0.11(BD:C) + 0.01(BD ² :C)	0.83
Beech Sm ^c	<i>Fagus grandifolia</i>	9	Summer	+0.84 + 1.53BD – 0.36S	0.69
			Winter	+0.46 + 1.57BD – 0.40S	0.69
Beech Lg ^d	<i>F. grandifolia</i>	2	Summer	5.04	NA
			Winter	4.57	NA
Hobblebush	<i>Viburnum lantanooides</i>	19	Summer	+4.44 + 0.89V + 0.05V ²	0.97
			Winter	+2.96 + 0.96V	0.94
Poplars	<i>Populus grandidentata</i> , <i>P. tremulooides</i>	21	Summer	–8.07 + 6.22BD – 0.71BD ²	0.83
			Winter	–8.98 + 6.26BD – 0.71BD ²	0.86
Cherries	<i>Prunus serotina</i> , <i>P. pensylvanica</i>	24	Summer	+11.49 + 2.19BD – 0.04BD ² – 2.02S + 1.36(BD:S) – 0.23(BD ² :S)	0.87
			Winter	–16.07 + 11.42BD – 1.47BD ² – 0.13S	0.79
Wild raisin	<i>Viburnum nudum cassinooides</i>	21	Summer	+9.11 + 0.99V – 0.01E – 0.02S	0.95
			Winter	+8.97 + 1.00V – 0.01E – 0.03S	0.94

^aBasal diameter < 55 mm; ^b Basal diameter ≥ 55 mm; ^cBasal diameter < 60 mm; ^dBasal diameter ≥ 60 m.

highest ranked model with lowest AIC_c score that satisfied model assumptions. Model assumptions were examined using the Shapiro-Wilk test for normality, Durbin-Watson test for autocorrelation, and Breusch-Pagan test for heteroskedasticity.

Estimating Range Capacity

We estimated available browse biomass for each cover type with Monte Carlo (MC) sampling (1000 iterations per strata) to account for variation in predictions at each scaling strata (individual plants, plots, transects, and cover types) using R statistical software Version 4.0.1 (R Core Team 2020). We were able to propagate uncertainties at multiple spatial scales by obtaining confidence intervals from the 1000 iterations per each scale. First, we applied allometric equations to predict the available browse biomass on each individual plant by species. We multiplied that prediction by the proportion of the browse on each individual plant species that fell within the defined sampling plot to account for incidences where the entire sampled plant did not fall within the plot. We then resampled predicted values using MC methods to create a grand mean for each individual plant. We summed the predicted biomass across all individuals of a species within each plot. Drawing from these values, a second MC sampling generated new values of plot-level biomass for each species, from which we derived a mean biomass per species per plot. Across each transect, we summed values of biomass per species/plot and conducted a third MC sampling to generate new values of transect-level biomass for each species. We summed predicted biomass values along transects per cover type, with a final MC sampling generating new values of cover type-level biomass for each species. We converted the final biomass estimates to kg/ha per species for inclusion in range capacity estimates for each cover type.

We used the FRESH modeling technique (Hanley et al. 2012) to quantify the range capacity of each forage and cover type for moose. We specified the model based on the energy and crude protein requirements of an adult female pregnant in winter and lactating in summer. To determine energetic requirements, the mean body weight (BW) for an adult female moose in this region was set to 350 kg based on conversion of field-dressed (carcass) BW reported in New Hampshire, Vermont, and Maine (unpublished data, K. Rines, New Hampshire Fish and Game Department) with the equation:

$$\text{Live Weight} = \text{Carcass Weight} \times 1.46 \quad (1)$$

(Crichton 1997)

We derived values for daily weight loss, dry matter intake, metabolizable energy requirements (ME), foraging time, and bite size from the literature (Table 2). Estimates of crude protein (CP) and digestible energy (DE) available in principle forage species were available from a related study of moose diets in the Park (Peterson et al. 2020). The FRESH model used an energy constraint based on ME requirements, but required DE values for the input of different forage species; the relationship was assumed as $ME \approx DE \times 0.82$ (D. Spalinger, author).

The FRESH model included an input called MAX that allowed the user to define the maximum amount of biomass of a browsed species that could be included in an individual's diet (Felton et al. 2020). We defined this from the field observed utilization rate of each species from previously conducted browse selection surveys (Peterson et al. 2020). We calculated a relative utilization index for each I species with the following equation (Gallant et al. 2004, Raffel et al. 2009, Harrison 2011):

$$U_i = \# \text{ browsed twigs} / \# \text{ available twigs} \quad (2)$$

Table 2. Nutritional requirements and foraging constraints set for a 350 kg, pregnant or nursing, female moose in the FRESH Cervid model used to estimate Animal Use Days per hectare (AUD/ha) by cover type in the Adirondack Park, New York.

Constraint	Season	Value	Formula	Sources
Daily weight loss	Both	0.4 kg/day		Renecker and Hudson 1989
Dry matter intake	Summer	11,570 g/day	$143 \times BW^{0.75}$	McArt et al. 2010, Renecker and Hudson 1989
	Winter	3075 g/day	$38 \times BW^{0.75}$	
Metabolizable energy	Summer	55,400 kJ/day	$0.82 \times (835 \text{ kJ} \times BW^{0.75})$	Schwartz et al. 1988, Renecker and Hudson 1989, Dungan et al. 2010
	Winter	27,827 kJ/day	$0.82 \times (124 \text{ kcal} \times BW^{0.75}) \times 0.29 \text{ kcal/kJ}$	
Crude protein	Summer	9.12%		Schwartz et al. 1987, VanBallenberghe and Miquelle 1990
	Winter	6.86%		
Foraging time	Summer	534 min/day		Risenhoover 1986, Dungan et al. 2010
	Winter	347 min/day		
Bite size	Summer	1.5 g dry mass		Moen 1995, Moen et al. 1997
	Winter	1.0 g dry mass		

U_i was quantified at the transect level and averaged for each species within each cover type. We further adjusted the available browse biomass value predicted for each cover type to account for changes in local moose browsing intensity (F_c) due to interfering vegetation (i.e., beech and conifer cover; Peterson et al. 2020). To do so, we calculated F_c at the cover type level by quantifying the average total biomass of principal browse species, percent cover of beech, and percent cover of conifer within each cover type, and determined the impacts on browse intensity with and without the effects of beech and conifer (Peterson et al. 2020). F_c was applied as a weight (summer = 0.81–0.99, winter = 0.94–0.98) to the biomass value for each forage species by cover type in the FRESH model. The estimates of Animal Use Days (AUD) supported by available browse were ultimately compared with and without the adjustment of F_c .

Applying point estimates for each component in the FRESH model, initial

estimates of AUD were achieved under 2 alternative constraints: 1) a ME constraint set at 55,400 kJ/day and 27,827 kJ/day for summer and winter, respectively, and 2) a CP constraint set at 9.12 and 6.86% for summer and winter, respectively (Regelin et al. 1985, Reese and Robbins 1994). For each scenario, we calculated total range capacity across the Park by multiplying the AUD/ha of each cover type by the areal extent of each type on the landscape. Comprehensive mapping of regenerating forest was lacking for the Park. Therefore, we estimated its coverage from field surveys that measured the proportion of regenerating forest within private inholdings that were classified *a priori* as conifer forest, upland deciduous/mixed forest, and lowland deciduous/mixed forest (Ferree and Anderson 2013); the proportions were 20, 21, and 4%, respectively. We divided the mean AUD by 180 days (length of the summer or winter season), multiplied this value by 0.2 to apply a cropping rate ensuring sufficient regeneration without

long-term damage to the range (Allen et al. 1987), and ultimately considered the season, constraint, and cover types producing the lowest mean AUD as most limiting to moose in the system.

Spatially-explicit estimates of AUD were determined by multiplying the estimated AUD/ha of a given cover type by the local proportion of that cover type within a defined area. Spatially-explicit estimates of moose density were available within a sample of 3×10 km blocks surveyed across the Park in winter 2016 (J. Hinton, SUNY-ESF, unpublished data). Survey blocks were excluded from consideration where reliable, on-the-ground information on regenerating timber cuts was unavailable, yielding 18 blocks for this comparison. We calculated AUD using the scenario indicated as most limiting for moose in each season. We also calculated total browse biomass available in each season within these 18 blocks. To quantify the strength of relationship between local AUD (or browse biomass) and moose density, we fit a linear model for each scenario (winter versus summer, protein versus energy constraint) and compared models by the variance explained.

Finally, we applied the FRESH model under the most limiting conditions to predict potential changes in AUD for moose under 3 scenarios of plausible future landscape changes in the region: 1) warmer and drier conditions leading to 10% conversion of wetland areas (open and wooded wetland types; 33,147 ha) to lowland mixed forest, 2) increased development leading to 10% conversion of coniferous and deciduous forests (176,193 ha) to non-habitat on private lands, and 3) increased timber harvest on private lands converting 2% of deciduous/mixed forest (30,276 ha) and 1% of conifer forest (2481 ha) to regenerating forest, a reasonable estimate based on consultation with local forest managers. We ran 1000 MC simulations in each scenario.

RESULTS

Allometric Models

We sampled 11–32 (ave. = 21) individual plants per species in each season and fit allometric models to 11 distinct plant groupings (Appendix 2 and 3). With the exception of large beeches ($n = 2$, intercept only model) and large maples ($n = 17$, elevation as sole predictor), basal diameter or volume metrics (with linear or nonlinear terms) were important predictors of available browse biomass of individual plants. We did not detect a difference in allometric relationships for any species among sampling years (models including year effects $\Delta AIC_c > 2.0$). All selected models met the assumptions of normally-distributed (SW = 0.90 – 0.98), independent (DW = 1.40 – 3.87), and homoscedastic errors (BP = 0.15 – 10.60; all $P > 0.05$), with the exception of the northern wild raisin (*Viburnum nudum cassanoides*) model in summer which indicated dependent errors (DW = 1.40, $P = 0.04$). In both seasons, all competing best models ($\Delta AIC_c < 2.0$) violated assumptions of either normally distributed, independent, or homoscedastic error. The first model that met all model assumptions was less supported ($\Delta AIC_c = 2.20$) than those with violations, but that model predicted values that differed from the best-supported model by $\sim 1\%$ only. Therefore, we chose to use the top model despite violating model assumptions.

Available Browse Biomass

Four species that were widespread in each cover type represented $\sim 70\%$ of available browse biomass in summer (Fig. 2); hobblebush (*Viburnum lantanoides*, 27.7%) and striped maple (*Acer pensylvanicum*, 23.8%) provided $\sim 50\%$ of biomass with red maple (11.4%) and yellow birch (9.2%) combining for $\sim 20\%$. Northern wild raisin (10.2%) and sugar maple (9.7%) also provided $\sim 20\%$ combined but were not distributed evenly

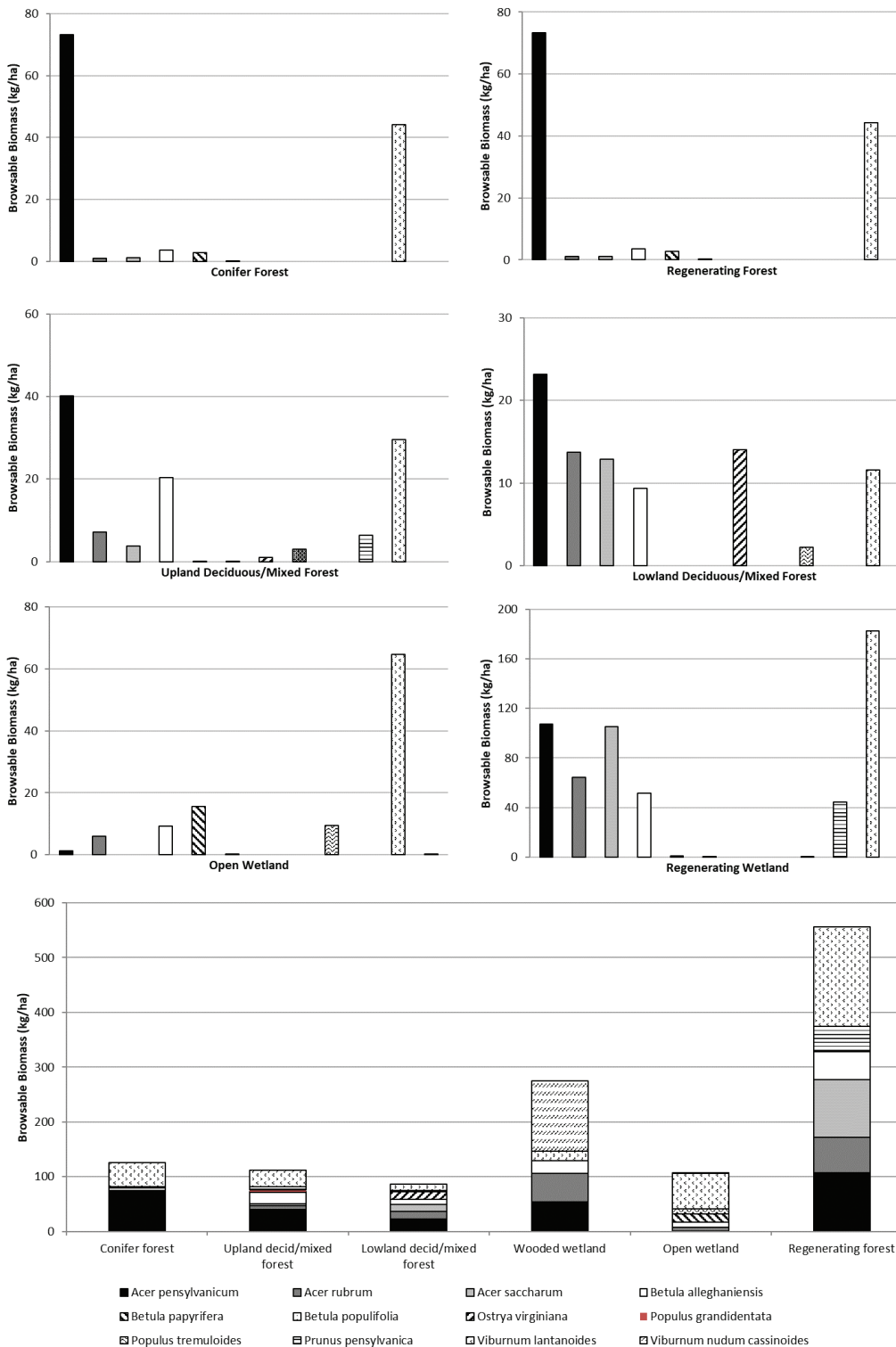


Fig. 2. Estimated density of browsable biomass (kg/ha) for moose during summer in the Adirondack Park, 2016–17. Estimates correspond to principal browse species only, those making up 95% of moose seasonal diets, with mean values reported by primary cover type.

across all cover types. In winter, balsam fir dominated browse availability (57.4%; Fig. 3) followed by striped maple (14.9%) and yellow birch (8.7%). Across cover types, the estimated reduction in browse intensity ranged from 2.3% (open wetland) to 18.5% (upland and lowland deciduous/mixed forest) in summer, and 1.1% (conifer forest) to 5.5% (open wetland) in winter.

By cover type, available browse biomass ranged from 87.0 (lowland deciduous/mixed forest) to 556.5 kg/ha (regenerating forest) during summer, and 146.7 (upland deciduous/mixed forest) to 376.0 kg/ha (wooded wetlands) during winter. Regenerating forest provided 2–6 × more available browse in summer than other cover types, and yielded 64% more browse than the dominant cover type (upland and lowland deciduous/mixed forest covering 63% of the landscape). In contrast, availability of winter browse biomass was more evenly distributed with wooded wetland (23.1%), open wetland (21.3%), and regenerating forest (18.5%) providing ~60% combined. Available browse within regenerating forest was dominated by yellow birch (38.4%) and several maple species (35.3%), whereas balsam fir (58.5–93.7%) was dominant in wetland types. In both seasons, available browse biomass was more homogeneous in regenerating forest than in other cover types (CV = 0.42 in summer and 0.23 in winter), as well as among transects in that type (CV = 0.13 in summer and 0.089 in winter).

Predicted Range Capacity

The distribution of cover types across the Park was dominated by deciduous/mixed forest (64% combined): 33.3% lowland deciduous/mixed forest (737,710 ha), 30.9% upland deciduous/mixed forest (685,396 ha), 10.4% conifer forest (230,043 ha), 10.2% forested wetland (225,280 ha), 4.6% regenerating forest (102,214 ha), and 4.4%

open wetland (97,557 ha). The summer range supported fewer adult female moose (0.00–5.97 AUD/ha across cover types) than the winter range (0.23–26.54 AUD/ha) (Table 3). Only upland deciduous/mixed forest and regenerating forest provided browse sufficient to meet the protein needs of lactating moose in summer. Regenerating forest supported 6 × more AUD/ha than upland deciduous/mixed forest based on protein requirements. Moreover, browse within regenerating forest and wooded wetland provided the most abundant sources of available energy in summer. Every habitat type produced sufficient browse in winter to meet the protein and energy requirements of pregnant moose due to the high use of balsam fir and the lower daily energetic requirement in winter relative to summer. In winter, the highest AUD was predicted within wooded and open wetlands because of the abundance of balsam fir.

We predicted the total available browse (under a protein constraint) in summer to support 457 ± 240 SD reproductive females when accounting for uncertainty (Table 4). Spatially-explicit estimates (within individual aerial survey blocks, $n = 18$) of summer AUD/ha under the crude protein constraint explained a moderate and significant amount of variation in the observed moose density via aerial surveys ($R^2 = 0.75$, $P < 0.01$; Fig. 4). Block-level density estimates for moose were less strongly related to AUD estimates under the summer energy constraint ($R^2 = 0.45$, $P < 0.01$), winter energy constraint ($R^2 = 0.36$, $P < 0.01$), and winter protein constraint ($R^2 = 0.12$, $P = 0.15$). Likewise, available browse biomass within each sampling block during summer showed a moderately strong relationship with estimated moose density in winter ($R^2 = 0.64$, $P < 0.01$), whereas browse biomass in winter was a poor predictor of winter moose density ($R^2 = -0.06$, $P = 0.90$).

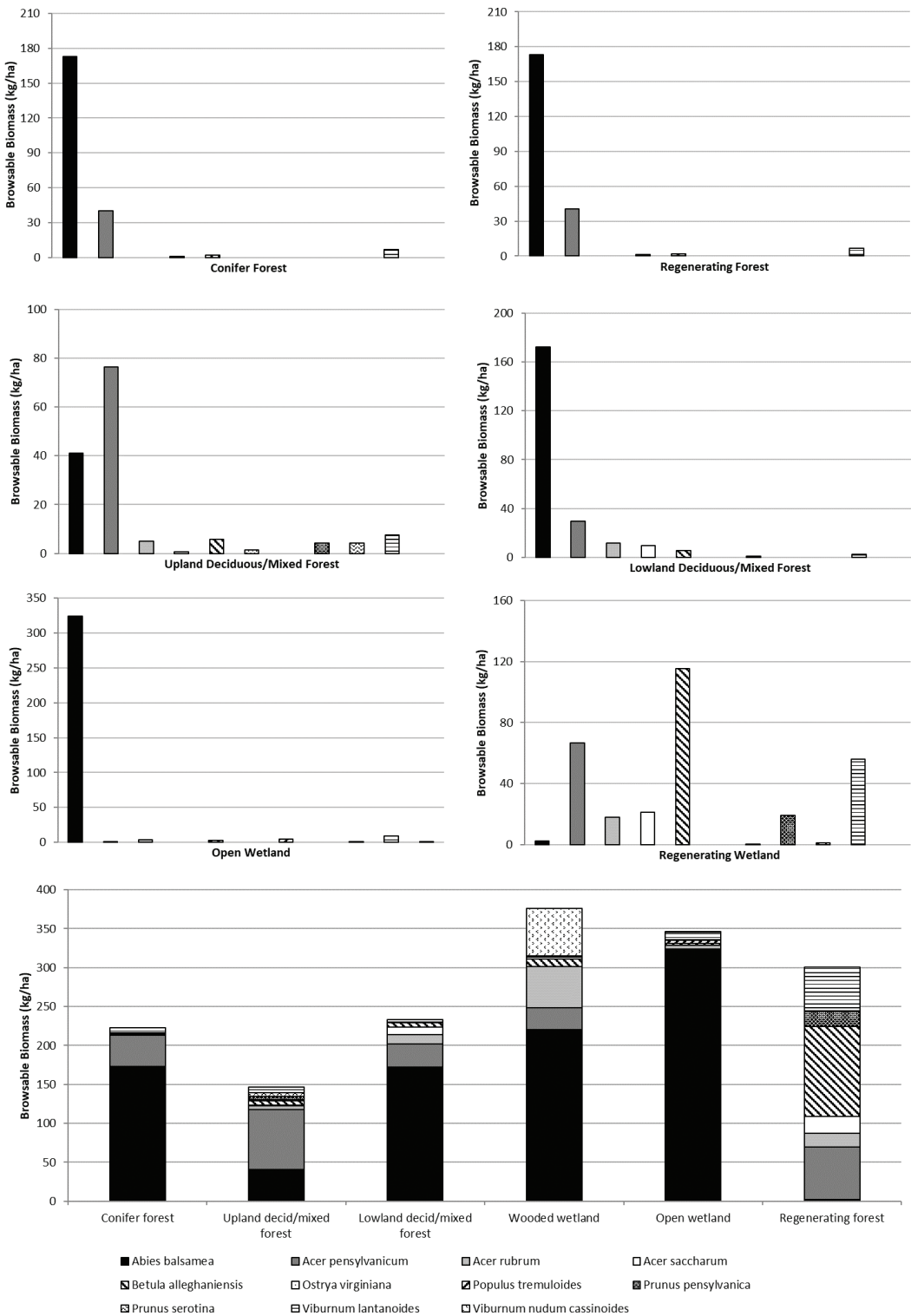


Fig. 3. Estimated density of browsable biomass (kg/ha) for moose during winter in the Adirondack Park, 2016–17. Estimates correspond to principal browse species only, those making up 95% of moose seasonal diets, with mean values reported by primary cover type.

Table 3. The estimated number of seasonal Animal Use Days (AUD) per hectare (with standard deviation) for moose in 6 different cover types within the Adirondack Park, New York. Error from biomass availability, nutritional content of browse and diet selection habits of moose (Peterson et al. 2020) were incorporated through a series of Monte Carlo simulations.

Cover type	Summer AUD		Winter AUD	
	Protein	Energy	Protein	Energy
Conifer forest	–	0.48 (0.52)	13.81 (11.14)	13.51 (11.17)
Upland decid/mixed forest	0.28 (0.23)	0.70 (0.34)	5.74 (3.30)	3.16 (2.69)
Lowland decid/mixed forest	–	0.71 (0.34)	16.18 (14.47)	15.84 (14.03)
Wooded wetland	–	5.97 (5.05)	26.02 (21.43)	15.93 (15.10)
Open wetland	–	0.57 (0.46)	23.74 (21.04)	26.54 (22.90)
Regenerating forest	1.95 (1.69)	5.61 (2.87)	11.28 (9.23)	0.23 (0.22)

Table 4. Estimates of Park-wide nutritional carrying capacity of reproductive female moose in Adirondack Park, New York by (A) total abundance and (B) density. Values shown incorporate error from biomass availability, nutritional quality of forage and diet selection habits (U_i) of moose. Browse intensity values (F_c) are also included in these estimates.

	A. Total moose				
	Summer		Winter		
	Crude Protein	Energy	Crude Protein	Energy	
Mean	456.5	3453.20	32897.70	26998.70	
SD	239.6	1267.10	12341.80	11612.10	
	B. Moose per Km ²				
	Mean	0.02	0.15	1.4	1.15
	SD	0.01	0.05	0.53	0.49

Landscape Changes Scenarios

We used summer protein constraint for our landscape change scenarios because it was identified as the most limiting factor for moose across season (summer and winter) and resource (crude protein and energy). In terms of model sensitivity, and in the absence of diet selectivity and ignoring model uncertainty, the potential reduction in browse intensity due to interfering vegetation alone yielded a point estimate for summer range capacity of 587 reproductive

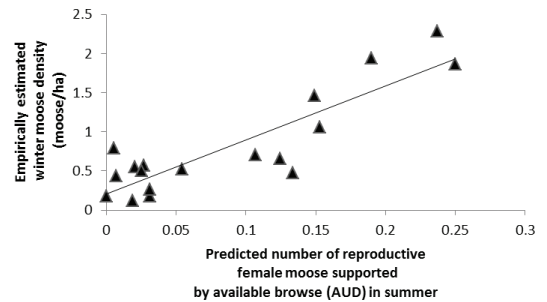


Fig. 4. Predicted number of reproductive female moose supported by available summer browse (Animal Use Days) within 18, 3×10 km² survey blocks (based on protein requirement) compared to the empirically-estimated density of moose in those blocks during winter 2016.

females. Accounting for diet selection, the estimates of summer AUD were reduced 82.2%, and accounting for interfering vegetation further reduced the estimates by 11.4%; combined, these factors reduced AUD 84.3%. Ultimately, uncertainty in diet selectivity explained the greatest proportion of total variance in the final estimates (ave. CV = 22% across types and scenarios). Uncertainty in the estimated crude protein content of species or in predicted biomass availability by cover type contributed minimally to the variance in final estimates (<1% each).

Removal of mature forest yielded the largest change in range capacity either by

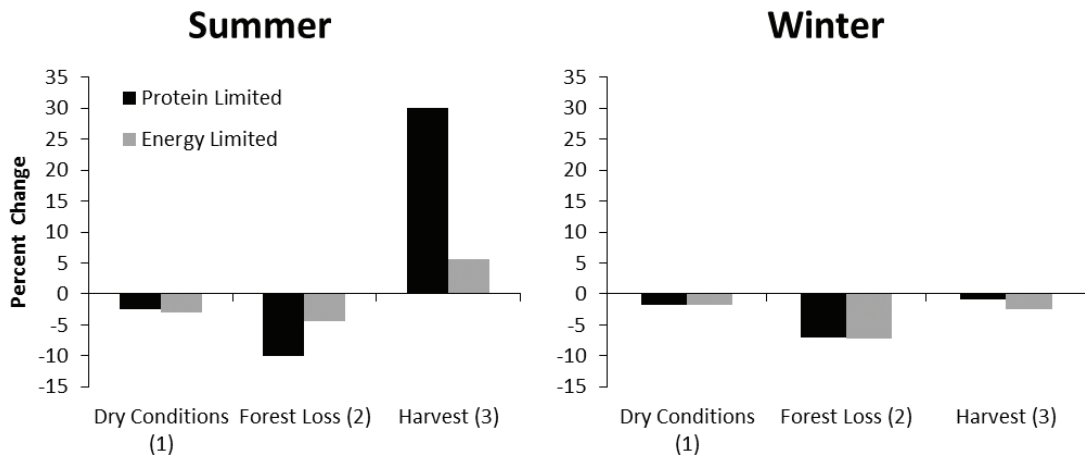


Fig. 5. Predicted changes in the total number of reproductive female moose supported by available browse in the Adirondack Park under 3 landscape change scenarios. Scenarios represent drying conditions leading to a 10% conversion of wooded and open wetland habitat to lowland deciduous/mixed forest, increased development leading to 10% conversion of conifer and deciduous/mixed forest to non-habitat, and increased timber harvest leading to 1% conversion of conifer forest and 2% conversion of deciduous/mixed forest to regenerating forest. Values indicate the percent change in the number of female moose relative to contemporary range conditions.

reducing capacity through conversion to non-habitat (development scenario) or increasing capacity through conversion to regenerating forest (timber harvest scenario; Fig. 5). In contrast, loss of wetlands (drier conditions scenario) or conversion of wetlands to lowland deciduous/mixed forest (the only scenario that adds additional forest) yielded minor impact (<5%) on range capacity. Models predicted that range capacity might increase by 30% in summer through harvest of 30,000 ha of mixed forest and 2400 ha of conifer forest. All landscape change scenarios predicted minimal reduction in winter range capacity (<~5%).

DISCUSSION

Our models indicate that the current and future moose population within the Park is constrained by summer protein availability associated with lack of early successional/regenerating forest. The summer population estimate of ~455 reproductive females (under a protein constraint) was surprisingly

similar to the total population estimate from winter aerial surveys (~700 moose; J. Hinton, SUNY College of Environmental Science and Forestry, unpublished data); more importantly, spatially-explicit estimates explained a substantial amount of variation in local moose density. We recognize that while leaves and stems of woody species dominate moose diets (Belovsky 1981), aquatic vegetation also provides measurable summer-fall forage when available (Crete and Jordan 1981). Because we did not account for aquatic vegetation in the models and wetlands are widespread and common in the Park (14.6% was classified as open or forested wetland), we presume that our estimates of summer range capacity are somewhat low. Conversely, our unreasonably large estimate of winter range capacity (>25,000 animals or >1 animal/km²) was biased high because we did not account for selectivity (Pastor and Danell 2003) within species and age classes of browse (e.g., balsam fir foliage), effects of secondary

compounds on limiting consumption of balsam fir (Parikh et al. 2017, Nosko et al. 2020), and the influence of snow depth on browse availability (Visscher et al. 2006). However, that winter browse would need to be reduced 99% to match the limitation on summer range arguably reflects the simple interaction of an abundance of balsam fir with low nutrient requirements in the winter model. Although sample size per modeled vegetative class was smaller than desirable, we did assess variation in available biomass production and palatability across both species and size classes by separating our samples by size and species when estimating AUD (Peterson et al. 2020). Despite certain limitations in our assumptions and sample sizes, we believe our data and analyses were sufficient to conclude that summer protein limitation is and will be the primary determinant of the stability and growth of the Park moose population.

Where this moose population stands with respect to potential nutritional carrying capacity remains an open question beyond the lack of regenerating forest habitat. The persistent, low density population is consistent with its stable, yet limited availability of summer forage protein, and not necessarily reflective of low recruitment and survival. Ungulate populations near carrying capacity trend toward reduced productivity (Couturier et al 2009, Wam et al. 2010), and the 3-year calf:cow ratio (0.5 ± 0.9 SD) from limited aerial sampling in the Park (NYS DEC, unpublished data) is considered moderate productivity (Kuzyk et al. 2018). This population is currently protected from harvest and without a major predator, with brainworm (*Parelaphostrongylus tenuis*) and liver fluke (*Fascioloides magna*) causing 12% of incidental natural mortality (K. Schuler, Cornell University College of Veterinary Medicine, unpublished data). Brainworm is somewhat of concern given

the high deer density around most of the Park and the current low-moderate deer density within.

The primary objective was to determine if nutritional limitation for moose occurs in the Park and our models indicate that the moose population is under summer protein constraint due to lack of optimal foraging habitat associated with regenerating forest. In nearby moose populations inhabiting mostly commercial forestland (Maine, New Hampshire, Vermont), optimal foraging habitat is generated continuously and used year-round (Dunfey-Ball 2019). Numerous regional studies have identified use and preference of regenerating forest in winter, investigated and measured winter browsing damage on valuable, regenerating deciduous species, and documented use of mature coniferous forest when mobility and activity is restricted temporarily in extreme winter conditions (Thompson et al. 1995, Scarpitti et al. 2005, Bergeron et al. 2011, Millette et al. 2014, Andreozzi et al. 2016). Thus, it is not surprising that constrained availability of summer biomass was correlated positively with winter moose density, and conversely, that winter browse biomass dominated by balsam fir was a poor predictor of winter moose density. Our inflated estimates of winter ADU reflect the high availability and presumed use of balsam fir in the model, and inadvertently minimized the effect of limited deciduous browse in regenerating forest that is preferred winter forage. That we found restricted seasonal forage/nutrition and low moose population density were linked in the Park reflects the direct relationship between availability of year-round optimal foraging habitat and population abundance (Peek 2007). Importantly, conversion of mature forests to regenerating stands would increase optimal and preferred forage in both summer and winter.

Legal harvest (hunting) is the most common tool for managing ungulate populations within their carrying capacity or to reduce over-populations. Instituting harvest of the small Park population is not feasible under current statutory constraints. Although the recent history of regional moose harvest is short-term (since the 1980s), harvest reductions were implemented by the mid-2000s in New Hampshire and Vermont despite conservative harvest rates in populations of multiple thousands of animals. In these small states, the interrelationships of moderate-high moose density, winter tick parasitism, and climate change have reduced productivity in primary moose range despite commercial private forests continuously producing optimal foraging habitat (Dunfey-Ball 2019, Jones et al. 2019, Pekins 2020, DeBow et al. 2021). In contrast, The Adirondack Park has a low density moose population, lack of timber harvest and optimal foraging habitat, and to date, unmeasured population impact from winter tick. Because the population is constrained by lack of optimal foraging habitat, strategic forest management (cutting) to address this limitation is desirable, yet that is also prohibited by statute in much of the Park. The regional population explosion of moose in the 1970–1990s reflected unprecedented harvest rates of spruce-fir forests in response to a spruce budworm infestation in the 1970–80s. Ironically, a trio of forest pests may provide a natural process to improve moose habitat in the Park on public lands through canopy openings in response to the current invasion by hemlock woolly adelgid, red pine scale (*Matsucoccus resinosa*), and again, the spruce budworm in the northeastern United States.

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APPENDICES

Appendix 1: Reclassification of Ecosystems defined by The Nature Conservancy's Terrestrial Habitat Map for the Northeastern US and Atlantic (Ferree and Anderson 2013). Ecosystems were assigned to either conifer, deciduous/mixed, wetland, wooded wetland or no-sampling based on ecosystem descriptions provided by Ferree and Anderson 2013. The deciduous/mixed class was further separated into upland and lowland forests, using a cutoff of 497 m in elevation.

TNC class	TNC ecosystem	Reclassification
Upland	Acadian Low Elevation Spruce-Fir-Hardwood Forest	Conifer
Upland	Acadian Sub-boreal Spruce Flat	Conifer
Upland	Acadian-Appalachian Alpine Tundra	No Sampling
Upland	Acadian-Appalachian Montane Spruce-Fir-Hardwood Forest	Conifer
Upland	Agriculture	No Sampling
Upland	Appalachian (Hemlock)-Northern Hardwood Forest: drier	Deciduous/Mixed
Upland	Appalachian (Hemlock)-Northern Hardwood Forest: moist-cool	Deciduous/Mixed
Upland	Appalachian (Hemlock)-Northern Hardwood Forest: typic	Deciduous/Mixed
Upland	Central Appalachian Dry Oak-Pine Forest	Deciduous/Mixed
Upland	Central Appalachian Pine-Oak Rocky Woodland	Deciduous/Mixed
Upland	Developed	No Sampling
Upland	Glacial Marine & Lake Mesic Clayplain Forest	Deciduous/Mixed
Upland	Great Lakes Alvar	No Sampling
Upland	Laurentian Acidic Rocky Outcrop	No Sampling
Upland	Laurentian-Acadian Acidic Cliff and Talus	No Sampling
Upland	Laurentian-Acadian Calcareous Cliff and Talus	No Sampling
Upland	Laurentian-Acadian Calcareous Rocky Outcrop	No Sampling
Upland	Laurentian-Acadian Northern Hardwood Forest: high conifer	Deciduous/Mixed
Upland	Laurentian-Acadian Northern Hardwood Forest: moist-cool	Deciduous/Mixed
Upland	Laurentian-Acadian Northern Hardwood Forest: typic	Deciduous/Mixed
Upland	Laurentian-Acadian Northern Pine-(Oak) Forest	Deciduous/Mixed
Upland	Laurentian-Acadian Pine-Hemlock-Hardwood Forest: moist-cool	Deciduous/Mixed
Upland	Laurentian-Acadian Pine-Hemlock-Hardwood Forest: typic	Deciduous/Mixed
Upland	Laurentian-Acadian Red Oak-Northern Hardwood Forest	Deciduous/Mixed
Upland	North-Central Appalachian Acidic Cliff and Talus	No Sampling
Upland	North-Central Appalachian Circumneutral Cliff and Talus	No Sampling
Upland	Northeastern Interior Pine Barrens	Conifer
Upland	Northern Appalachian-Acadian Rocky Heath Outcrop	No Sampling
Upland	Open Water	No Sampling
Upland	Shrubland/grassland; mostly ruderal shrublands, regenerating clearcuts	No Sampling
Wetland	Boreal-Laurentian Bog: Isolated/small stream	Wetland
Wetland	Boreal-Laurentian-Acadian Acidic Basin Fen: Undifferentiated	Wetland
Wetland	Glacial Marine & Lake Wet Clayplain Forest: Undifferentiated	Wetland
Wetland	Laurentian-Acadian Alkaline Conifer-Hardwood Swamp: Isolated	Wooded Wetland
Wetland	Laurentian-Acadian Alkaline Conifer-Hardwood Swamp: Lake/pond: any size	Wooded Wetland

Appendix 1 (continued)

Appendix 1 (continued): Reclassification of Ecosystems defined by The Nature Conservancy's Terrestrial Habitat Map for the Northeastern US and Atlantic (Ferree and Anderson 2013). Ecosystems were assigned to either conifer, deciduous/mixed, wetland, wooded wetland or no-sampling based on ecosystem descriptions provided by Ferree and Anderson 2013. The deciduous/mixed class was further separated into upland and lowland forests, using a cutoff of 497 m in elevation.

TNC class	TNC ecosystem	Reclassification
Wetland	Laurentian-Acadian Alkaline Conifer-Hardwood Swamp: Smaller river floodplain/riparian	Wooded Wetland
Wetland	Laurentian-Acadian Freshwater Marsh: Isolated	Wetland
Wetland	Laurentian-Acadian Freshwater Marsh: Lake/pond: any size	Wetland
Wetland	Laurentian-Acadian Freshwater Marsh: Smaller river floodplain/riparian	Wetland
Wetland	Laurentian-Acadian Large River Floodplain: Acidic Swamp	Wetland
Wetland	Laurentian-Acadian Large River Floodplain: Alkaline Conifer-Hardwood Swamp	Wooded Wetland
Wetland	Laurentian-Acadian Large River Floodplain: Conifer-Hardwood Acidic Swamp	Wooded Wetland
Wetland	Laurentian-Acadian Large River Floodplain: Floodplain Forest	Wooded Wetland
Wetland	Laurentian-Acadian Large River Floodplain: Freshwater Marsh	Wetland
Wetland	Laurentian-Acadian Large River Floodplain: Wet Meadow-Shrub Swamp	Wetland
Wetland	Laurentian-Acadian Wet Meadow-Shrub Swamp: Isolated	Wetland
Wetland	Laurentian-Acadian Wet Meadow-Shrub Swamp: Lake/pond: any size	Wetland
Wetland	Laurentian-Acadian Wet Meadow-Shrub Swamp: Smaller river floodplain/riparian	Wetland
Wetland	North-Central Appalachian Acidic Swamp: Isolated	Wetland
Wetland	North-Central Appalachian Acidic Swamp: Lake/pond: any size	Wetland
Wetland	North-Central Appalachian Acidic Swamp: Smaller river floodplain/riparian	Wetland
Wetland	North-Central Appalachian Large River Floodplain: Acidic Swamp	Wetland
Wetland	North-Central Appalachian Large River Floodplain: Acidic Swamp	Wetland
Wetland	North-Central Appalachian Large River Floodplain: Freshwater Marsh	Wetland
Wetland	North-Central Appalachian Large River Floodplain: Rich Swamp	Wetland
Wetland	North-Central Appalachian Large River Floodplain: Rich Swamp	Wetland
Wetland	North-Central Appalachian Large River Floodplain: Wet Meadow-Shrub Swamp	Wetland
Wetland	North-Central Interior and Appalachian Acidic Peatland: Undifferentiated	Wetland
Wetland	North-Central Interior and Appalachian Rich Swamp: Isolated	Wetland
Wetland	North-Central Interior and Appalachian Rich Swamp: Lake/pond: any size	Wetland
Wetland	North-Central Interior and Appalachian Rich Swamp: Smaller river floodplain/riparian	Wetland
Wetland	North-Central Interior Wet Flatwoods: Undifferentiated	Wetland
Wetland	Northern Appalachian-Acadian Conifer-Hardwood Acidic Swamp: Isolated	Wooded Wetland
Wetland	Northern Appalachian-Acadian Conifer-Hardwood Acidic Swamp: Lake/pond: any size	Wooded Wetland
Wetland	Northern Appalachian-Acadian Conifer-Hardwood Acidic Swamp: Smaller river floodplain/riparian	Wooded Wetland

Appendix 2: Model selection table for allometric equations describing browse biomass availability on individual tree and shrub species for moose in Adirondack Park, New York during summer. Models for large (>60 mm diameter) American beech are not displayed, as the small sample size warranted an intercept only model. Only candidate models carrying >1% of cumulative model weight are displayed.

Small Maples	Main effects	Interactions	df	logLik	AIC _c	delta	weight
	BD		3	-14.22	36.62	0.00	0.19
	BD2		3	-14.40	36.99	0.38	0.16
	BD+D		4	-12.82	37.65	1.03	0.11
	BD2+D		4	-13.04	38.07	1.46	0.09
	BD+S		4	-13.26	38.52	1.90	0.07
	BD2+S		4	-13.36	38.73	2.11	0.07
	BD+BD2		4	-14.09	40.18	3.56	0.03
	BD+ES		4	-14.14	40.27	3.66	0.03
	E+BD		4	-14.17	40.34	3.73	0.03
	BD2+ES		4	-14.30	40.60	3.99	0.03
	E+BD2		4	-14.35	40.70	4.08	0.02
	E+BD+D		5	-12.08	40.83	4.21	0.02
	E+BD2+D		5	-12.38	41.42	4.81	0.02
	BD+BD2+D		5	-12.70	42.06	5.44	0.01
	BD+D+S		5	-12.71	42.09	5.48	0.01
	BD+D+ES		5	-12.81	42.29	5.67	0.01
	BD2+D+S		5	-12.88	42.43	5.81	0.01
Large Maples	E		3	-24.63	57.10	0.00	0.21
	N		3	-25.38	58.61	1.51	0.10
	CC+E		4	-23.76	58.85	1.75	0.09
	E+BD		4	-24.01	59.36	2.26	0.07
	E+N		4	-24.22	59.77	2.67	0.06
	E+S		4	-24.59	60.51	3.41	0.04
			2	-28.06	60.98	3.88	0.03
	BD+N		4	-24.95	61.24	4.14	0.03
	BD2+N		4	-24.95	61.24	4.14	0.03
	CC+N		4	-25.02	61.36	4.26	0.03
	BD2		3	-26.97	61.79	4.69	0.02
	BD		3	-26.99	61.83	4.73	0.02
	S+N		4	-25.32	61.98	4.88	0.02
	S		3	-27.16	62.16	5.06	0.02
	CC+E+N		5	-23.48	62.42	5.32	0.01
	CC+E+BD2		5	-23.68	62.82	5.72	0.01
	CC+E+BD		5	-23.69	62.83	5.73	0.01
	CC+E+S		5	-23.71	62.88	5.78	0.01
	E+BD2+N		5	-23.74	62.94	5.84	0.01
	E+BD+BD2		5	-23.74	62.94	5.84	0.01
	E+BD+N		5	-23.77	62.99	5.89	0.01

Appendix 2 (continued)

Appendix 2 (continued): Model selection table for allometric equations describing browse biomass availability on individual tree and shrub species for moose in Adirondack Park, New York during summer. Models for large (>60 mm diameter) American beech are not displayed, as the small sample size warranted an intercept only model. Only candidate models carrying >1% of cumulative model weight are displayed.

Small Maples	Main effects	Interactions	df	logLik	AIC _c	delta	weight
	CC		3	-27.67	63.19	6.09	0.01
Birches	CC+BD+BD2+S	BD × S	7	-30.16	80.21	0.00	0.09
	CC+BD+BD2+S	BD2 × S	7	-30.42	80.73	0.52	0.07
	CC+BD+BD2	CC × BD	6	-32.86	81.93	1.72	0.04
	CC+BD+BD2	CC × BD+CC × BD2	7	-31.43	82.75	2.54	0.03
	CC+BD+BD2+D+S	BD × S	8	-29.76	83.52	3.31	0.02
	CC+E+BD+BD2	CC × E+CC × BD	8	-29.78	83.56	3.35	0.02
	CC+BD+BD2	CC × BD2	6	-33.68	83.57	3.35	0.02
	CC+E+BD+BD2+S	CC × E+CC × S	9	-27.54	83.66	3.45	0.02
	CC+BD+BD2+S+N	BD × S	8	-29.88	83.76	3.55	0.02
	CC+E+BD+BD2+S	BD × S	8	-29.96	83.91	3.70	0.01
	CC+BD+BD2+D+S	BD2 × S	8	-29.96	83.92	3.70	0.01
	CC+BD+BD2+S	CC × S	7	-32.03	83.96	3.75	0.01
	CC+E+BD+BD2+D+S	CC × E+CC × S	10	-25.14	84.03	3.82	0.01
	CC+BD+BD2+S	BD × S+BD2 × S	8	-30.11	84.21	4.00	0.01
	CC+BD+S	BD × S	6	-34.01	84.23	4.01	0.01
	CC+BD+BD2+S	CC × S+BD × S	8	-30.12	84.24	4.02	0.01
	CC+BD+BD2+S	CC × BD2+BD × S	8	-30.12	84.25	4.04	0.01
	CC+BD+BD2+S+N	BD2 × S	8	-30.14	84.29	4.07	0.01
	CC+BD+BD2+S	CC × BD+BD × S	8	-30.15	84.30	4.09	0.01
	CC+E+BD+BD2+S	CC × E+BD × S	9	-27.94	84.47	4.26	0.01
	BD+BD2+S		5	-35.86	84.58	4.37	0.01
Hobblebush	E+V+V2		5	1	11.8	0	0.12
	E+V+V2	ExV	6	0.778801	12.3	0.5	0.09
	E+V		4	0.740818	12.4	0.6	0.09
	V		3	0.704688	12.5	0.7	0.08
	V+V2		4	0.57695	12.9	1.1	0.07
	CC+E+V+V2		6	0.367879	13.8	2	0.04
	CC+V+V2		5	0.286505	14.3	2.5	0.03
	E+V	ExV	5	0.201897	15	3.2	0.02
	CC+V		4	0.201897	15	3.2	0.02
	A+A2+H		5	0.19205	15.1	3.3	0.02
	A+A2+H		5	0.19205	15.1	3.3	0.02
	A+A2+V		5	0.19205	15.1	3.3	0.02
	E+V+V2		5	0.182684	15.2	3.4	0.02
	H+V		4	0.157237	15.5	3.7	0.02
	A+V		4	0.157237	15.5	3.7	0.02
	A+H		4	0.157237	15.5	3.7	0.02
A+H		4	0.157237	15.5	3.7	0.02	

Appendix 2 (continued)

Appendix 2 (continued): Model selection table for allometric equations describing browse biomass availability on individual tree and shrub species for moose in Adirondack Park, New York during summer. Models for large (>60 mm diameter) American beech are not displayed, as the small sample size warranted an intercept only model. Only candidate models carrying >1% of cumulative model weight are displayed.

Small Maples	Main effects	Interactions	df	logLik	AIC _c	delta	weight
	V+V2		4	0.157237	15.5	3.7	0.02
	H+V+V2		5	0.157237	15.5	3.7	0.02
	A+V+V2		5	0.157237	15.5	3.7	0.02
	CC+E+V		5	0.149569	15.6	3.8	0.02
	E+V+V2+D		6	0.142274	15.7	3.9	0.02
	E+A+A2+V		6	0.142274	15.7	3.9	0.02
	E+A+A2+H		6	0.142274	15.7	3.9	0.02
	E+A+A2+H		6	0.142274	15.7	3.9	0.02
	CC+E+V+V2	ExV	7	0.122456	16	4.2	0.01
	E+A+V		5	0.116484	16.1	4.3	0.01
Aspens	BD+BD2		4	-13.39	37.28	0.00	0.33
	CC+BD+BD2		5	-12.53	39.06	1.77	0.14
	BD+BD2+S		5	-12.98	39.95	2.67	0.09
	E+BD+BD2		5	-13.35	40.70	3.42	0.06
	BD+BD2+D		5	-13.39	40.77	3.49	0.06
	CC+E+BD+BD2		6	-11.94	41.88	4.60	0.03
	CC+BD+BD2+S		6	-12.19	42.39	5.10	0.03
	CC+BD+BD2	CC × BD2	6	-12.36	42.72	5.44	0.02
	CC+BD+BD2	CC × BD	6	-12.41	42.82	5.54	0.02
	CC+BD+BD2+D		6	-12.53	43.05	5.77	0.02
	BD+BD2+D+S		6	-12.76	43.52	6.23	0.01
	BD+BD2+S	BD2 × S	6	-12.97	43.94	6.66	0.01
	E+BD+BD2+S		6	-12.97	43.94	6.66	0.01
	BD+BD2+S	BD × S	6	-12.97	43.95	6.67	0.01
Cherries	BD+BD2+S+Ea	BD × S+BD2 × S	8	-24.88	75.36	0.00	0.16
	E+BD+BD2+S	BD × S+BD2 × S	8	-25.41	76.42	1.06	0.09
	CC+E+BD+BD2+S	BD × S+BD2 × S	9	-23.70	78.26	2.90	0.04
	E+BD+BD2+S		6	-30.91	78.77	3.41	0.03
	E+BD+BD2+S+N	BD × S+BD2 × S	9	-23.99	78.83	3.47	0.03
	BD+BD2+S		5	-32.84	79.01	3.65	0.03
	E+BD+BD2+S+Ea	BD × S+BD2 × S	9	-24.10	79.05	3.69	0.03
	CC+E+BD+BD2+S	CC × BD2+BD × S+BD2 × S	10	-21.34	79.60	4.24	0.02
	BD+BD2+S	BD × S+BD2 × S	7	-29.41	79.81	4.45	0.02
	BD+BD2+D+S+Ea	BD × S+BD2 × S	9	-24.64	80.13	4.77	0.01
	BD+BD2+S+Ea	BD × S+BD × Ea+BD2 × S	9	-24.72	80.30	4.94	0.01
	BD+BD2+S+Ea+N	BD × S+BD2 × S	9	-24.73	80.32	4.96	0.01
	BD+BD2+S+Ea		6	-31.69	80.33	4.97	0.01
	BD+BD2+S+Ea	BD × S+BD2 × S+BD2 × Ea	9	-24.75	80.36	5.00	0.01

Appendix 2 (continued)

Appendix 2 (continued): Model selection table for allometric equations describing browse biomass availability on individual tree and shrub species for moose in Adirondack Park, New York during summer. Models for large (>60 mm diameter) American beech are not displayed, as the small sample size warranted an intercept only model. Only candidate models carrying >1% of cumulative model weight are displayed.

Small Maples	Main effects	Interactions	df	logLik	AIC _c	delta	weight
	CC+BD+BD2+S+Ea	BD × S+BD2 × S	9	-24.81	80.48	5.12	0.01
	E+BD+BD2+D+S	BD × S+BD2 × S	9	-24.86	80.59	5.23	0.01
	CC+E+BD+BD2+S	CC × BD+CC × BD2	9	-24.87	80.59	5.23	0.01
	CC+E+BD+BD2+S	CC × BD+BD × S+BD2 × S	10	-21.98	80.88	5.52	0.01
Northern Wild Raisin	E+V+S		5	-2.69	19.40	0.00	0.14
	E+V+N		5	-3.07	20.10	0.75	0.09
	CC+E+V		5	-3.27	20.50	1.15	0.08
	CC+V		4	-5.54	21.60	2.20	0.05
	CC+E+V+S		6	-1.98	21.90	2.56	0.04
	CC+E+V+N		6	-2.00	22.00	2.61	0.04
	E+V+S	E × V	6	-2.00	22.00	2.62	0.04
	E+V+N	E × V	6	-2.11	22.20	2.84	0.03
	CC+V	CC × V	5	-4.18	22.40	2.98	0.03
	E+V+S	V × S	6	-2.22	22.40	3.06	0.03
	E+V	E × V	5	-4.26	22.50	3.13	0.03
	E+V+S+N		6	-2.39	22.80	3.39	0.03
	CC+E+V	CC × V	6	-2.56	23.10	3.73	0.02
	E+V+N	E × V+V × N	7	-0.61	23.80	4.45	0.02
	CC+V+S		5	-4.93	23.90	4.47	0.01
	E+V+N	V × N	6	-3.03	24.10	4.67	0.01
	V+S+N	V × N	6	-3.03	24.10	4.68	0.01
	CC+E+V	E × V	6	-3.08	24.20	4.78	0.01
	CC+E+V	CC × E	6	-3.27	24.50	5.15	0.01
	CC+V+N	V × N	6	-3.34	24.70	5.29	0.01
Small Beech	BD+S		4	-8.435	34.9	0	0.14
	S		3	-12.516	35.8	0.96	0.09
	Intercept		2	-14.96	35.9	1.05	0.08
	E		3	-12.771	36.3	1.47	0.07
	BD+E		4	-9.527	37.1	2.18	0.05
	BD		3	-13.411	37.6	2.75	0.04
	BD+D		3	-14.667	40.1	5.26	0.01
	CC		3	-14.827	40.5	5.58	0.01

Appendix 3: Model selection table for allometric equations describing browse biomass availability on individual tree and shrub species for moose in Adirondack Park, New York during winter. Models for large (>60 mm diameter) American beech are not displayed, as the small sample size warranted an intercept only model. Only candidate models carrying >1% of cumulative model weight are displayed.

Small Maples	Main effects	Interactions	df	logLik	AICc	Delta	Weight
	BD+S		4	-15.11	42.21	0.00	0.39
	BD		3	-18.36	44.89	2.68	0.10
	BD+S	BD × S	5	-14.37	45.40	3.19	0.08
	BD+D		4	-16.76	45.51	3.30	0.07
	E+BD+S		5	-14.79	46.25	4.04	0.05
	BD+D+S		5	-15.03	46.73	4.52	0.04
	BD+S+N		5	-15.10	46.88	4.66	0.04
	BD+N		4	-17.53	47.06	4.84	0.03
	BD+D+N		5	-15.22	47.11	4.90	0.03
	BD+N	BD × N	5	-15.58	47.83	5.62	0.02
	E+BD		4	-18.14	48.27	6.06	0.02
	BD+D	BD × D	5	-16.30	49.27	7.06	0.01
	S		3	-20.56	49.30	7.09	0.01
	E+BD+D+N		6	-13.41	49.31	7.10	0.01
Large Maples	E		3	-25.00	57.85	0.00	0.44
	E+BD		4	-24.53	60.39	2.54	0.12
	E+N		4	-24.94	61.21	3.36	0.08
	E+S		4	-24.99	61.31	3.46	0.08
	N		3	-26.86	61.56	3.71	0.07
			2	-28.86	62.58	4.73	0.04
	E+BD		5	-23.98	63.41	5.56	0.03
	BD		3	-27.94	63.72	5.87	0.02
	S		3	-28.00	63.85	6.00	0.02
	BD+N		4	-26.47	64.28	6.43	0.02
	E+BD+N		5	-24.52	64.49	6.64	0.02
	E+BD+S		5	-24.52	64.49	6.64	0.02
	S+N		4	-26.75	64.84	6.99	0.01
	E+S+N		5	-24.93	65.32	7.47	0.01
Striped Maple	BD+D	BD × D	5	-18.85	53.70	0.00	0.47
	BD+BD2+D	BD × D	6	-17.60	56.53	2.83	0.11
	BD+BD2+D	BD2 × D	6	-17.60	56.54	2.84	0.11
	BD+D+S	BD × D	6	-18.64	58.60	4.91	0.04
	BD2+D+S	BD2 × D	6	-19.28	59.90	6.20	0.02
Birches	CC+BD+BD2	CC × BD+CC × BD2	7	-34.00	87.90	0.00	0.17
	CC+BD+BD2	CC × BD	6	-36.43	89.06	1.16	0.09
	CC+BD+BD2+S	BD × S	7	-35.04	89.98	2.08	0.06
	CC+BD+BD2+D	CC × BD	7	-35.63	91.15	3.25	0.03
	CC+BD+BD2+S	BD2 × S	7	-35.65	91.19	3.29	0.03

Appendix 3 (continued)

Appendix 3 (Continued): Model selection table for allometric equations describing browse biomass availability on individual tree and shrub species for moose in Adirondack Park, New York during winter. Models for large (>60 mm diameter) American beech are not displayed, as the small sample size warranted an intercept only model. Only candidate models carrying >1% of cumulative model weight are displayed.

Small Maples	Main effects	Interactions	df	logLik	AICc	Delta	Weight
	CC+E+BD+BD2	CC × BD+CC × BD2	8	-33.62	91.24	3.34	0.03
	CC+BD+BD2	CC × BD2	6	-37.53	91.26	3.36	0.03
	CC+BD+BD2+D	CC × BD+CC × BD2	8	-33.70	91.40	3.50	0.03
	CC+BD+BD2+N	CC × BD+CC × BD2	8	-33.70	91.41	3.51	0.03
	BD+BD2+S	BD × S	6	-37.82	91.85	3.95	0.02
	CC+BD+BD2+S	CC × BD+CC × BD2	8	-33.95	91.90	4.00	0.02
	BD+BD2+S	BD2 × S	6	-38.12	92.44	4.54	0.02
	CC+BD+BD2+N	CC × BD	7	-36.29	92.47	4.57	0.02
	CC+BD+BD2+S	CC × BD	7	-36.36	92.61	4.71	0.02
	CC+E+BD+BD2	CC × BD	7	-36.43	92.74	4.84	0.01
	CC+BD+BD2+D+S	BD × S	8	-34.41	92.82	4.92	0.01
	CC+BD+BD2+D	CC × BD+BD2 × D	8	-34.42	92.84	4.93	0.01
	CC+BD+BD2+S	BD × S+BD2 × S	8	-34.46	92.92	5.02	0.01
	CC+BD+BD2+S+N	BD × S	8	-34.51	93.01	5.11	0.01
	CC+BD+BD2+D	CC × BD2	7	-36.70	93.30	5.40	0.01
Hobblebush	V		3	-7.68	22.95	0.00	0.13
	CC+E	CC × V	6	-2.79	24.57	1.62	0.06
	CC+E+V2	CC × V	7	-0.52	25.23	2.28	0.04
	H		4	-7.20	25.25	2.30	0.04
	E		4	-7.26	25.37	2.42	0.04
	E+V2		5	-5.38	25.38	2.43	0.04
	CC		4	-7.30	25.45	2.50	0.04
	D		4	-7.44	25.74	2.79	0.03
	CC	CC × V	5	-5.60	25.82	2.87	0.03
	CC+V2	CC × V	6	-3.65	26.31	3.35	0.03
	H+V2		5	-5.85	26.31	3.36	0.03
	V2+D		5	-5.99	26.59	3.64	0.02
	E+H		5	-5.99	26.60	3.65	0.02
	CC+E+V2		6	-4.22	27.44	4.49	0.01
	CC+V2	CC × V2	6	-4.30	27.59	4.64	0.01
	E+H+V2		6	-4.46	27.93	4.98	0.01
Aspens	BD+BD2		4	-12.05	34.60	0.00	0.33
	BD+BD2+D		5	-11.32	36.63	2.04	0.12
	BD+BD2+S		5	-11.45	36.91	2.31	0.10
	CC+BD+BD2		5	-11.82	37.65	3.05	0.07
	E+BD+BD2		5	-12.04	38.07	3.48	0.06
	BD+BD2+D	BD2 × D	6	-10.83	39.67	5.07	0.03
	BD+BD2+D	BD × D	6	-10.89	39.79	5.19	0.02

Appendix 3 (continued)

Appendix 3 (Continued): Model selection table for allometric equations describing browse biomass availability on individual tree and shrub species for moose in Adirondack Park, New York during winter. Models for large (>60 mm diameter) American beech are not displayed, as the small sample size warranted an intercept only model. Only candidate models carrying >1% of cumulative model weight are displayed.

Small Maples	Main effects	Interactions	df	logLik	AICc	Delta	Weight
	CC+BD+BD2+D		6	-11.16	40.32	5.72	0.02
	E+BD+BD2+S		6	-11.21	40.41	5.82	0.02
	BD+BD2+D+S		6	-11.23	40.46	5.86	0.02
	CC+BD+BD2+S		6	-11.28	40.56	5.97	0.02
	E+BD+BD2+D		6	-11.31	40.63	6.03	0.02
	BD+BD2+S	BD × S	6	-11.35	40.69	6.10	0.02
	BD+BD2+S	BD2 × S	6	-11.35	40.69	6.10	0.02
Cherries	BD+BD2+S		5	-34.04	81.41	0.00	0.15
	E+BD+BD2+S		6	-32.76	82.46	1.05	0.09
	BD+BD2+S+E		6	-32.88	82.69	1.28	0.08
	CC+E+BD+BD2+S	CC × BD2	8	-28.80	83.21	1.79	0.06
	BD+BD2+D+S		6	-33.67	84.28	2.87	0.04
	CC+BD+BD2+S	CC × BD2	7	-31.65	84.31	2.89	0.04
	CC+E+BD+BD2+S		7	-31.67	84.35	2.93	0.03
	BD+BD2+S	BD2 × S	6	-33.82	84.57	3.16	0.03
	BD+BD2+S+N		6	-33.87	84.69	3.27	0.03
	CC+BD+BD2+S		6	-33.98	84.90	3.48	0.03
	E+BD+BD2+S+N		7	-32.23	85.46	4.05	0.02
	E+BD+BD2+S	BD2 × S	7	-32.27	85.54	4.12	0.02
	E+BD+BD2+S+E		7	-32.45	85.90	4.49	0.02
	E+BD+BD2+D+S		7	-32.51	86.02	4.60	0.01
	E+BD+BD2+S	E × BD2	7	-32.53	86.05	4.64	0.01
	CC+BD+BD2+S+E	CC × BD2	8	-30.36	86.32	4.90	0.01
	BD+BD2+S+E+N		7	-32.81	86.62	5.20	0.01
	CC+BD+BD2+S+E		7	-32.83	86.66	5.24	0.01
	BD+BD2+S+E	BD2 × E	7	-32.84	86.67	5.26	0.01
	BD+BD2+S+E	BD2 × S	7	-32.86	86.72	5.31	0.01
	BD+BD2+D+S+E		7	-32.87	86.74	5.33	0.01
Northern Wild Raisin	E+V+S		5	-5.57	25.15	0.00	0.20
	E+V+N		5	-6.58	27.15	2.01	0.07
	CC+E+V		5	-6.85	27.71	2.56	0.06
	E+V+S	E × V	6	-5.02	28.03	2.89	0.05
	CC+V		4	-8.83	28.16	3.01	0.04
	CC+E+V+S		6	-5.14	28.28	3.13	0.04
	E+V+S	V × S	6	-5.18	28.37	3.22	0.04
	E+V+S+N		6	-5.46	28.92	3.77	0.03
	E+V	E × V	5	-7.64	29.27	4.13	0.03
	CC+V	CC × V	5	-7.71	29.42	4.27	0.02

Appendix 3 (continued)

Appendix 3 (Continued): Model selection table for allometric equations describing browse biomass availability on individual tree and shrub species for moose in Adirondack Park, New York during winter. Models for large (>60 mm diameter) American beech are not displayed, as the small sample size warranted an intercept only model. Only candidate models carrying >1% of cumulative model weight are displayed.

Small Maples	Main effects	Interactions	df	logLik	AICc	Delta	Weight
	CC+E+V+N		6	-5.80	29.60	4.46	0.02
	CC+V+S		5	-7.90	29.81	4.66	0.02
	E+V+N	E × V	6	-5.91	29.82	4.68	0.02
	V+S+N	V × N	6	-6.04	30.09	4.94	0.02
	V		3	-11.41	30.22	5.08	0.02
	V+S		4	-9.90	30.30	5.16	0.02
	CC+E+V	CC × V	6	-6.30	30.60	5.46	0.01
	E+V+N	E × V+V × N	7	-4.13	30.87	5.73	0.01
Small Beech	BD+S		4	-8.914	35.8	0	0.14
	S		3	-12.83	36.5	0.64	0.1
	Intercept		2	-15.5	37	1.17	0.08
	CC		3	-13.11	37	1.2	0.08
	BD+CC		4	-10.04	38.1	2.25	0.05
	BD		3	-14.1	39	3.17	0.03
	D		3	-15.19	41.2	5.35	0.01