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Moose Foraging in the Temperate Forests of Massachusetts: a Natural Re-Wilding Experiment

A thesis presented by

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to

the Graduate School of Arts and Sciences

In Partial Fulfillment of the Requirements for the Degree

of

Master in Forest Science

Harvard University
Cambridge, Massachusetts

June 2006

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Abstract

The “re-wilding” of ecosystems with extirpated large mammals has become a focus of recent scientific and conservation initiatives; however, it is unclear how proposed re-introductions will influence systems that are often vastly different from those that occurred before these animals were extirpated. Moose, the northeast’s largest Holocene browser, have recently expanded across southern New England’s temperate forest landscape after an absence of 200 years, realizing a natural re-wilding experiment. Moose have been well-studied throughout the boreal forest biome; however, because they are rare today in temperate forests, almost nothing is known of their ecology, behavior, or potential impacts to these ecosystems. This study investigated patterns of winter moose browse in order to: (1) gain insight into the likely influences of this herbivore on the vegetation patterns of the region; and (2) to identify the most important habitat features influencing moose winter foraging activity at a landscape and site scale. Two large forested watersheds in Central Massachusetts were sampled for moose browse, habitat features, and disturbances including forest harvesting and human activity. Chi-square and t-tests were used to identify browse species preferences of moose, and step-wise multiple regression was used to identify habitat variables that are strong predictors of browse intensity. Hardwoods and hemlock were favored over white pine, and browse intensity was significantly and positively related to forest harvesting, elevation, swamps, and distance to human settlement. The results from this study suggest that in the winter months, moose populations are concentrating in remote, elevated areas that are broken by swamps and have intensive forest harvests. In areas that support high moose densities, selective browsing, particularly in

regenerating harvests, could promote less favored species like white pine at the expense of hardwoods and hemlock. The strong association between moose and forest harvesting indicates that recolonizing megafauna may interact with novel human conditions and disturbances to impact ecosystems differently than in the past. Nonetheless, habitat loss and climate change may ultimately preclude the long-term viability of moose and its impacts to this region.

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To Brooke for enduring two years of this project with
cheerfulness and encouragement

Acknowledgements

Funding for this project was provided by the Anna B. Bliss Fund & Living Diorama Scholarship Fund and the Harvard University Program for Training and Research in Ecology from the Andrew W. Mellon Foundation. Special thanks to my advisor, David Foster for giving me the opportunity to pursue this study and for his meticulous editing that improved the quality of this paper immensely. My sincere thanks also to Glenn Motzkin for many in-depth conversations about this study and for his detailed and helpful editing of the manuscript. I wish all graduate students could have a committee member as sharp, devoted, and helpful as Glenn. I am also grateful to John McDonald for his encouragement and helpful correspondence throughout the process. Thanks also to Todd Fuller for helpful suggestions and to Aaron Ellison and Rob McDonald for statistical assistance. Others who provided knowledgeable correspondence include Dan Clark and Bill Woytek, and I thank Josh Rapp and Dan Wells for field assistance and for use of photos. Finally, I'd like to acknowledge my talented and dedicated MFS classmates who supported and inspired me along the way: Posy Busby, Brian DeGasperis, and Brooks Mathewson.

Introduction

During the past several decades, accumulating research has shown that large mammals (>45 kg), often interacting with fire and climate, can profoundly shape their ecosystems (McNaughton 1988, Post 1999; Knapp et al. 1999); and consequently in the absence of megafauna, ecosystems may be substantially altered (Zimov et al. 1995). This recognition has sparked a number of recent initiatives to "re-wild" parts of Europe, North America, and Siberia with original megafauna or with closely related proxies (Kirby 2004, Dinerstein and Irvin 2005, Donlan 2005, Zimov 2005, Martin 2005). Although the distribution and impacts of large mammals are often closely linked to habitat variation (McNaughton 1988, Peek 1997), the ecological implications of re-introduction efforts are hard to predict for species that have long been extirpated from a region. Thus, with the exception of a few examples such as wolf restoration in Yellowstone National Park, USA (Smith et al. 2003), the specific impacts of re-wilding initiatives remain speculative.

In southern New England, a natural re-wilding of large mammals has taken place over the past several decades, concomitant with regional afforestation after abandonment of agricultural land in the second half of the 19th century and changes in social attitudes and hunting regulations (Foster et al. 2002). White-tailed deer (*Odocoileus virginianus*) and black bear (*Ursus americanus*), along with numerous smaller mammals, have increased dramatically during this time period (Foster et al. 2002, CT DEP unpublished data); and during the past 10-15 years moose (*Alces alces*) have re-colonized the region after a ~200 year absence. Moose populations are increasing rapidly, and current estimates of 600-800 resident animals in southern New England (Masswildlife, CT DEP unpublished data) are at least as high as estimates for pre-European settlement populations (Vecellio et al. 1993, Godin 1977). Moose originally colonized southern New England at least 2200 years ago (Faunmap), and at the time of European settlement in the 17th century, they were relatively common in Massachusetts, though apparently scarce in Connecticut and Rhode Island (Vecellio 1993, Godin 1977). Unrestricted hunting and habitat loss throughout the 17th and 18th centuries caused the extirpation of moose and numerous other large animals throughout southern New England by about 1800 (Godin 1977).

Due to this early extirpation, we have no information about moose habitat preferences or foraging behavior in the oak-pine and hemlock forests of southern New England and little insight into their likely influence on forest dynamics and vegetation composition as they become re-established in this region. Analogy may be drawn from studies of white-tailed deer, which have been shown to suppress seedling regeneration, particularly conifers, causing structural and compositional changes to temperate forests of eastern North America (Healy 1997, Augustine and McNaughton 1998). However, despite overlaps in diet (Ludewig and Bowyer 1985), deer and moose have evolved different foraging strategies (Renecker and Schwartz 1997), and therefore deer impacts may not be a reliable predictor of future moose impacts.

Moose have a circumpolar distribution and occupy broad northern expanses that are largely uninhabited by people (Telfer 1984). Throughout their range, moose are strongly associated with regenerating woody vegetation in areas that have been burned, logged or otherwise disturbed (Peek 1997, Maier et al. 2005). In turn, selective browsing by moose in boreal regions may substantially alter forest structure, composition, and soil nutrient levels at both patch and landscape scales (Pastor et. al. 1988, Pastor et al. 1998, Persson et al. 2005). In southern New England, selective logging is the most widespread and common disturbance creating young, regenerating forests (Kittredge et al. 2003) and may play an important role in controlling landscape-level impacts of moose on forest ecosystem patterns and dynamics.

Moose are potentially limited by at least three interrelated factors in southern New England: climate, human development, and white-tailed deer. Average temperatures in the region frequently exceed those that generate heat stress in moose, and the area supports much greater populations of humans and white-tailed deer than the boreal zone. (NOAA, Schwartz and Renecker 1997). Moose are broadly tolerant of human settlement and activity (Telfer 1984); however, it is unknown how they may respond to the high human densities that occur across southern New England. White-tailed deer carry a parasitic meningeal worm (*Parelaphostrongylus tenuis*) that has been linked to infection and mortality in moose (Lankester and Samuel 1997). However, factors potentially limiting the moose population may be offset by reduced predation, as two of the moose's three chief natural predators, wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) are absent, whereas the third, black bear, occurs at low but expanding numbers in the region.

In this study I documented moose foraging patterns in a novel habitat type: the temperate forests of central Massachusetts, USA. My main objectives were (1) to quantify browse preferences to gain insights into the likely influences of moose on the vegetation of this region and (2) to identify the most important habitat features influencing moose foraging activity at a landscape and site scale. To accomplish these ends, I examined browse and availability of individual plant species in two large forested areas in relationship to forest type, forest structure, forest harvesting intensity and age, physiography and elevation, deer densities, distance from development, distance to water, and distance to conifer cover.

Study Area

The Quabbin and Ware River Watershed forests in the Central Uplands of Massachusetts, USA (Fig. 1) were selected for investigation for several reasons: they are believed to support the highest moose densities in southern New England (B. Woytek pers. comm.); they have considerable topographic and forest variation and support active harvesting regimes (Kittredge et al. 2003); and Quabbin Watershed has relatively fine-scale deer density data that are unavailable for most other areas in southern New England (McDonald et al. unpublished manuscript).

Figure 1. Study area: Quabbin and Ware River Watersheds, Massachusetts, USA. Study sites denoted by white circle with black dot in middle (Aerial Photography by MassGIS and NASA)

Quabbin Watershed Forest

Quabbin Reservation, the largest tract of conservation land in southern New England (Kittredge et al. 2003), forms the core of the 22,000 ha Quabbin Watershed Forest and envelops the 10,000 hectare Quabbin Reservoir (Fig. 1). Soils are primarily till-derived and acidic, and forests are predominantly oak-pine with lesser amounts of hemlock, sugar maple-ash, forested wetlands, and conifer plantations. (Massachusetts DCR unpublished data). Open wetlands comprise ~ 2-3% of the land area (McDonald et al. unpublished manuscript), and three branches of the Swift River drain through the area into Quabbin Reservoir. Elevations range from approximately 135-380 meters with higher elevations to the west side. Quabbin Reservation is closed to public vehicles and development but has an extensive network of unpaved woods roads. Moose colonized the Quabbin watershed about 12 years ago (B. Spencer pers. comm.), and the current population is estimated at 100 animals. Deer numbers have been maintained at approximately 2-7km^2 during the period of moose colonization (McDonald et al. unpublished manuscript), but as recently as the late 1980's were substantially higher (10-17km^2) (Healy 1997), leading to the initiation of an annual deer hunt in 1991.

Ware River Watershed Forest

The 9600 hectare Ware River Reservation, located some 10-12 kilometers east of the eastern edge of Quabbin Reservation (Fig. 1), forms the core of this watershed forest. It consists of glacial till-covered uplands interspersed with extensive valley outwash deposits that underlay 1400 hectares of wetlands (~9% of the study area). Two branches of the Ware River and the Burnshirt River dissect these forest lands and merge to form the Ware River inside the Reservation. Elevations in the watershed range from about

200-360 meters. The Reservation is undeveloped but has a network of unpaved woods roads and trails; unlike the Quabbin, many of these roads are open to public vehicular access. Oak-pine forests and forested wetlands are the most common forest cover types with lesser amounts of hemlock and conifer plantations (Massachusetts DCR unpublished data). Moose colonized the Ware River watershed about 12 years ago and are estimated at 150 animals today (D. Clark, H. Eck pers. comm.). Deer densities are estimated to be 6km^2 (D. Clark pers. comm.) and were continuously hunted throughout the 20th century.

Methods

Study Site Selection

To sample a wide range of forest types and ages, plots were established following a stratified random design by (1) forest type - four upland types: hemlock, white pine, mixed oak, and sugar maple-ash; and three wetland types: red maple swamp, conifer swamp, and terrace floodplain forest (Thompson and Sorenson 2000, Swain and Kearsley 2001, Kearsley 1999, Golet et al. 1993); and (2) recent harvesting history (harvested vs. unharvested since 1984 for upland sites only). At least 10 sites were sampled for each forest type and harvesting stratum (Gotelli and Ellison 2004), which were identified on state forest type GIS layers (Massachusetts DCR unpublished data) and a statewide forest harvesting database (McDonald et al. 2006). In addition, 10 oak hilltops were sampled to broaden the range of topographical positions. In cases where field visits indicated that the vegetation and harvesting history of a site did not agree with the GIS layers, the site was sampled and assigned to the proper stratum. To ensure independence of plots, sample locations were separated by a minimum distance of 700 meters, a distance based on the mean daily movements of moose in Minnesota (Phillips et al 1973). A total of 156 sites met these sampling criteria and were divided between the two watersheds in approximate proportion to the relative forest area of each property.

Vegetation Surveys

Each study site consisted of two 100 m^2 circular plots for sampling moose browse and tall shrub and tree density and composition. All trees >2.5 cm DBH were recorded by species and DBH, and all tall shrubs greater than 1.8 meters high were recorded by species. In a nested 10 m^2 circular subplot within each 100 m^2 plot, all tree stems <2.5 cm DBH were recorded by species to determine seedling density and composition (Higgins et al. 1996, Degraaf and Yamasaki 2001). The center of the two 100 m^2 plots were 30 m apart, and data from the two plots were pooled for each site.

Moose Browse Surveys

At each site, moose browse was assessed on trees and shrubs. To distinguish moose from deer foraging, I only recorded browse above 1.8 m, the height limit for white-tailed deer foraging (Curtis and Sullivan 2001). Moose forage at all heights between 0-3 m, but feeding trials in Sweden showed that on >80% of deciduous tree species they consume the most browse between 1.5 and 2.5 m (Bergstrom and Danell 1986). I assumed that recording browse above 1.8 would exclude most deer browse but still capture the predominant foraging activity of moose.

In each 100m^2 plot, all woody stems with live twigs between 1.8 and 3 meters were recorded by species and if browsed or not. Only twigs that were unequivocally browsed were recorded as “yes” (Plate 1). Bark-stripped stems >1.8 m high were also recorded as “browsed” (Plate 2). Seedlings and saplings pulled or walked down and snapped along the major stem were also noted (Plate 3). Moose predominantly feed on leaves of deciduous woody plants and aquatic vegetation in summer and twigs and bark in winter and early spring (Renecker and Schwartz 1997, Pastor et al. 1998). Therefore, my data capture late fall to early spring foraging.

Plate 1. Mature hemlock twig browsed by moose in Quabbin Reservation. (Photo by Dan Wells)

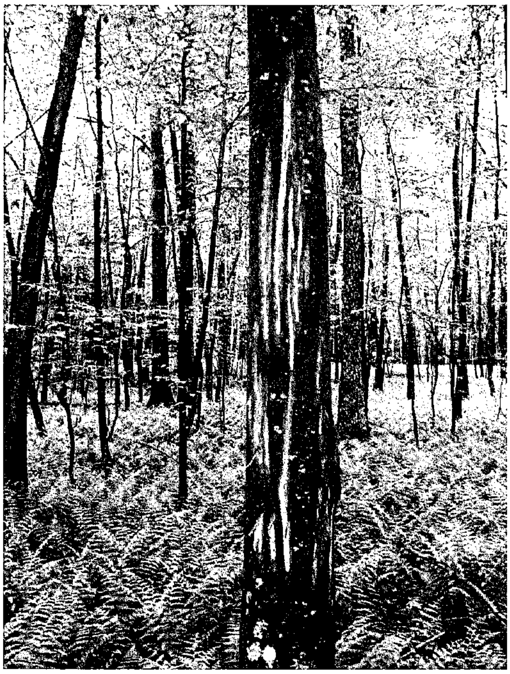

Plate 2. Red maple tree bark-stripped by moose Prescott Peninsula, Quabbin Watershed. (Photo by the author)

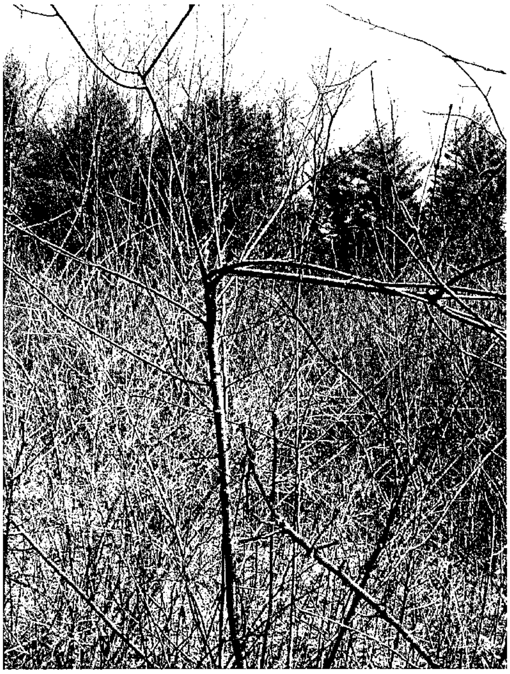

Plate 3. Black cherry sapling snapped by moose in Ware River Watershed. (Photo by the author)

Moose Browse Intensity Index

To standardize "browse intensity" across different forest types and ages, I developed a browse index for each site. The browse index is the sum of the relative proportion of stems browsed and the relative density of stems browsed. These values were calculated as follows for each site:

$$1.\ \text{Relative proportion of stems browsed} = \frac{\text{browsed/available stems}}{\text{highest ratio of browsed/available stems at any site}} \times 100$$

$$2.\ \text{Relative density of stems browsed} = \frac{\text{number of browsed stems}}{\text{largest number of browsed stems at any site}} \times 100$$

Browse index values therefore had a potential of 0-200, and I established a minimum of 5 available stems for a site to be included in the Browse Index calculation.

Explanatory Variables

Nineteen predictor variables were selected for analysis in relation to moose browse intensity. Three were related to forest structure and harvesting (the categorical variable, harvested or unharvested, forest harvest intensity {mboard feet of wood removed/hectare} and tall shrub density). Six variables were related to vegetation composition (relative basal area of red maple (*Acer rubrum*), white pine (*Pinus strobus*), sugar maple (*Acer saccharum*), oak (*Quercus* spp.), spruce (*Picea* spp), and hemlock (*Tsuga canadensis*). One was related to deer density (Quabbin deer densities by town (McDonald et al. unpublished manuscript). One was related to human settlement (distance to development (1 km max). MassGIS definitions of "developed" land were used, which includes residential, industrial, commercial, transportation, waste disposal, and recreation sites. Two were related to proximity to important land cover features (distance to water and distance to conifer cover (≥.5 hectares) (MassGIS; Thompson and Stewart 1997). Three categorical variables were related to topographic and hydrologic position (wetland forest as defined by MassGIS, hilltop, and swamp forest). Three broad geographic metrics were included (elevation, latitude, and landscape (Ware River or Quabbin)) to reflect the potential for moose foraging activity to be explained by broader spatial variables and factors.

Statistical Analysis

Stepwise multiple regression was used to analyze browse intensity (dependent variable) in relation to the 19 independent variables. Two multiple regression models were created: (1) for all 156 sites; (2) for 77 sites within Quabbin Reservation alone (to include deer densities as a predictor which were only available for Quabbin). Multi-collinearity was examined for all variables using correlation tables, and in all but three cases R values were <.28 (Graham 2003) (Appendix A). Analyses with and without these correlated variables demonstrated that they had no impact on the final model. To test for browse preferences among the individual plant species, chi square analysis was used to compare proportions of browsed vs. available stems between different tree species. To test for browse preferences of young versus mature trees, a t-test was used to compare the mean DBH of browsed stems vs. unbrowsed stems of each species.

Results

Moose browse occurred at 95 of 156 sites (61%) with intensity index values of 0 to 143. Browse frequency was similar between Ware River (65%) and Quabbin (60%); however mean intensity was higher at Ware River (though not significantly (P=0.06). Harvested sites (mean BI = 33) were browsed more intensively than unharvested upland sites (mean BI = 20) (P=0.01). Wetland forests (BI = 39) were browsed more intensively than unharvested upland sites (P=0.0004). Among wetland forests, swamps (mean BI= 60) were browsed more intensively than floodplains (mean BI = 11) (P =0.01). Moose browsed a total of 36 tree and shrub species, 23 of which have not been previously documented to be eaten by moose (Renecker and Schwartz 1997) (Appendix B). Among species that occurred in ≥10 different browsed sites, hemlock (50%), red maple (49%), witch hazel (*Hamamelis virginiana*) (44%), gray birch (*Betula populifolia*)(44%), and winterberry (*Ilex verticillata*) (43%) had the highest proportion of browsed stems, whereas white ash (*Fraxinus americana*) (5%), white pine (14%), and sugar maple (22%) had the lowest. Among seedlings and saplings of major tree species, hemlock, red maple, black cherry (*Prunus serotina*), red oak, and black birch all had significantly higher proportions of browsed stems than white pine (P≤0.001). (Fig. 2a). In addition, hemlock, red maple, and black cherry had higher proportions of browsed stems than black birch. For hemlock and sugar maple, browsed stems were significantly larger than unbrowsed stems (P=0.02, P=0.007) (Fig. 2b), whereas there was no size difference between browsed and unbrowsed red maple, red oak, and white pine. Bark-stripping was most frequent on red maple and chestnut (*Castanea dentata*) (Fig. 3a and

Appendix C), while gray birch had the highest frequency of snapped stems (Figure 3b and Appendix D).

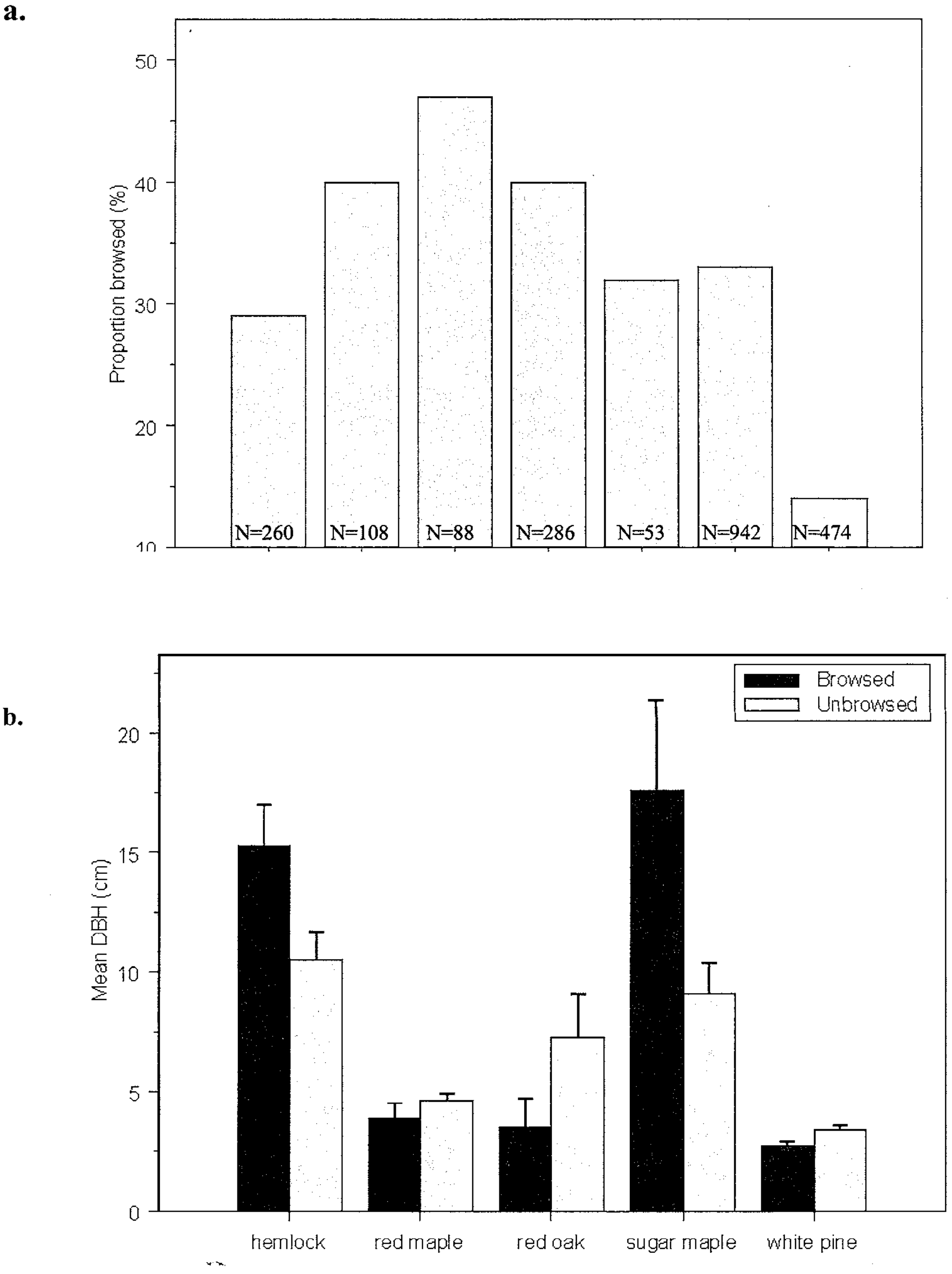

Figure 2. (a) Proportions of moose browse on seedlings and saplings of major tree species (N≥50). Six taxa had significantly higher proportion of browsed stems than white pine (P≤0.001); (b) Browse in relation to individual tree species size. Browsed hemlock (P=0.02) and sugar maple (P=0.007) stems were significantly larger than unbrowsed stems. All species included occurred in at least 10 different sites.

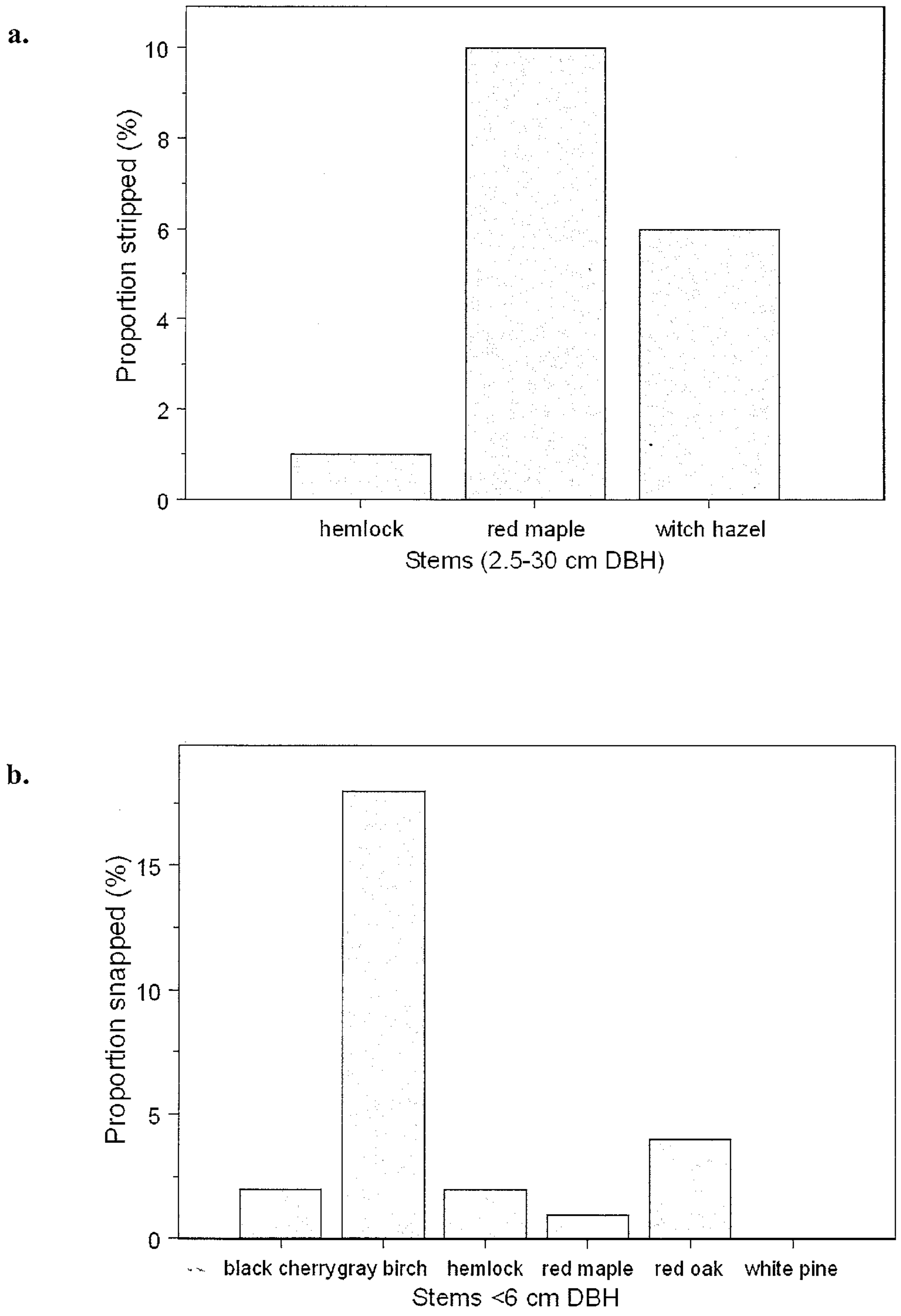

Figure 3. Proportions of stems (a) bark-stripped and (b) snapped by moose. Species occurred in at least 9 different sites. Proportions calculated from 95 sites where moose sign was present.

Multiple Regression Analysis of all 156 sites

In the final model, four of the nineteen variables were significant predictors of browse intensity ($P<0.05$) with positive coefficients (distance to development ($P=.0008$), harvested forests ($P=0.0006$), elevation ($P=0.0001$), and swamp forests ($P=0.02$ (Table 1). The model explained 26% of the variation in browse intensity. Analyses for interactions among vegetation composition and these 4 significant coeffiecients showed that relative basal area of hemlock had a negative interactive effect with harvested forests ($P=0.04$) and red maple had an interactive effect with swamp forests ($P=0.03$).

Table 1. Final stepwise multiple regression model for moose browse intensity at all sites

```
Coefficients:
                          Value Std. Error  t value Pr(>|t|)
           (Intercept) -28.8576  16.5579    -1.7428   0.0836
             elevation   0.2229   0.0533     4.1834   0.0001
                 swamp  14.9204   6.4063     2.3290   0.0213
           tall shrubs   0.4160   0.2800     1.4860   0.1396
distance conifer cover  -0.0175   0.0118    -1.4852   0.1398
               harvest   9.6159   2.7454     3.5025   0.0006
      distance Develop   0.0264   0.0077     3.4208   0.0008

Residual standard error: 29.6 on 137 degrees of freedom
Multiple R-Squared: 0.263
F-statistic: 8.148 on 6 and 137 degrees of freedom, the p-value is 1.533e-007
```

Multiple regression analysis including estimated deer densities

For the Quabbin Reservation sites, where deer densities were available, two positive coefficients (elevation: $P=0.0007$ and harvest intensity: $P = 0.0000$) (Fig. 4) were correlated with browse intensity. Deer density was not a significant correlate. The model explained 37% of the variation in browse intensity.

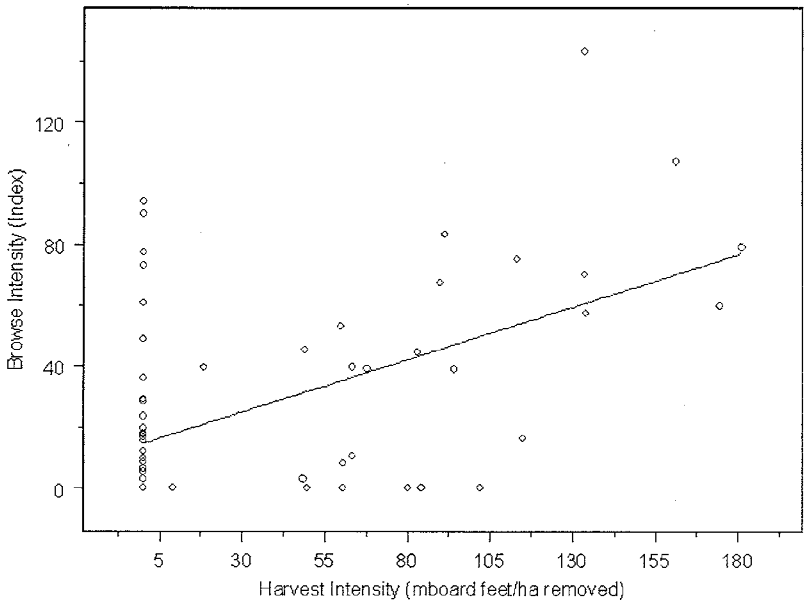

Figure 4. Browse intensity in relation to harvest intensity in the Quabbin Reservation.

Discussion

Throughout the boreal regions of North America, moose browse a great diversity of woody plants (130 taxa documented) but show strong preferences for only a few (Renecker and Schwartz 1997). Balsam fir (*Abies balsamea*) comprises 60-75% of the moose's winter diet in some areas (McLaren and Peterson 1994, Ludewig and Bowyer 1985), while spruce are avoided (Pastor et al. 1988). Deciduous taxa such as willow (*Salix* spp.), aspen (*Populus* spp.), and birch (*Betula* spp.) are also favored browse (Renecker and Schwartz 1997). My results indicate a parallel pattern among temperate forest species, as one dominant conifer (hemlock) and a few deciduous species (red maple, black cherry, and witch hazel) were heavily browsed while a second major conifer species (white pine) was largely avoided (Fig. 2a, Appendix B). These temperate species are absent from most of the moose's range (http://na.fs.fed.us/spfo/pubs/silvics), and black cherry, witch hazel, and winterberry have not been previously documented to be eaten by moose (Renecker and Schwartz 1997).

Parallel to moose influences in the boreal forest, extended periods of selective browsing could exert large effects on forest composition and structure in southern New England forests. In some boreal areas, moose have shifted forest composition from hardwood to red spruce (Pastor et al. 1993, Thompson and Curran 1993, Peek 1997) and suppressed balsam fir for decades (Thompson and Curran 1993, McLaren and Peterson 1994). In southern New England, where hemlock appears to be a predominant winter food, hemlock regeneration and future abundance could become suppressed in mixed forests. As reported for fir, impact to hemlock may be inversely related with hemlock densities (Thompson and Curran 1993, Peterson 1995, Appendix E). Hemlock's slow growth rate in the understory, where it may require up to 30 years to surpass 3 m in height (Vasiliauskas and Aarssen 1999), may increase its vulnerability to browsing pressure.

Forest harvesting and the future of white pine

In the late 19th century, selective grazing by livestock on hardwoods in abandoned pastures played an important role in the establishment of white pine stands in southern New England (Bromley 1935). Locally, an establishing moose population could exert a parallel effect on white pine establishment by selectively browsing hardwoods after cutting. Forest harvesting of low-to-medium intensity is widespread across much of southern New England with public lands more intensively harvested (Kittredge et al. 2003, McDonald et al. 2006). A compositional shift to white pine may be reduced by the faster regeneration rate of trees in temperate compared to boreal forests yet aided by the small scale of Massachusetts harvests (average 15 ha). These harvests contrast with fires and clearcuts in the boreal zone that can be on average almost 3 orders of magnitude and 4 times larger respectively (Hunter 1993, Environmental Canada). Large-scale and dense regeneration tends to mitigate the effects of moose browsing even in areas of very high moose density (Thompson and Curran 1993, Peterson 1995). A trend toward white pine may also be aided by P. *strobus's* relatively flexible stem compared to some hardwoods. Moose preferentially feed on the leaders of seedlings and saplings including white pine (Bryant and Kuropat 1980, Appendix E), often pulling stems down to reach the tips. Hardwoods commonly snap in this process (Appendix D); however, no snapped white pines were observed in this study.

Winter Browse Preferences and Plant characteristics

Moose generally forage less selectively in winter when food quality and availability is low (Edenius et al. 2002); nonetheless, the results from this study indicate that moose exhibit strong selectivity among and within plant taxa during the winter months. One reason for this may be to avoid excessive lignin intake, as high lignin content greatly increases rumen turnover time (Schwartz and Renecker 1997). Foliar chemistry data from Massachusetts show that hemlock, the most preferred browse species from this study, has a much lower lignin content (and slightly lower protein content) than white pine -- the least preferred browse species (http://www.folchem.sr.unh.edu/).

Another reason for selectivity may be to avoid plant toxins. In subarctic regions, moose select mature growth forms over juvenile forms of the same species in winter because of lower levels of secondary compounds in older trees (Bryant and Kuropat 1980). However, Swihart and Piccone (1998) found plant toxins to be higher in mature than juvenile hemlocks in Connecticut (although at very low levels overall). These authors also found higher nitrogen content in mature trees, as well as a preference for mature trees by deer, suggesting that relative nitrogen content may be an important driver of winter selection by moose of larger hemlock and sugar maples.

A preference for larger hemlocks and sugar maples in this study may also result from larger individuals of these species generally having more available browse than smaller stems. The similarity in size between browsed and unbrowsed red maple, white pine, and oaks may be related to a different growth form, as mature individuals of these species pruned their lower branches more completely than hemlock or sugar maple, leaving fewer large trees with twigs within the reach of moose.

Elevation

The relationship between elevation and moose browsing activity over only ~200 m of relief is intriguing and may be related to minor differences in temperature and vegetation (Rasche 1958, Kanda et al. 2005). Elevated forested sites in Central Massachusetts generally have longer growing seasons and fewer spring and fall frosts than adjacent valley sites (Rasche 1958). Browsing at higher elevations could reflect behavior to maximize the availability of nutritious browse in fall before nutrients are transferred from twigs to roots and in early spring when the reverse occurs (Schwartz and Renecker 1997).

Greater browsing at elevated sites may also indicate greater time spent in these sites, due to their advantage for thermoregulation. Higher elevation forested sites in Central Massachusetts generally have lower maximum (daytime) and mean temperatures than valley sites (Rasche 1958, Kanda et al. 2005). The moderating effect of elevation on temperature could be important to moose, as average winter temperatures in central

Massachusetts frequently exceed the reported heat stress threshold for moose (Schwartz and Renecker 1997), although the extent to which heat stress thresholds differ across the geographic range of moose is unknown.

Human Development

Browse intensity declined with increasing proximity to human development especially in the Ware River Watershed where the northern forests are interspersed with residential development and considerably less heavily browsed than areas where development is prohibited. This result contrasted with studies in Alberta and Alaska (Maier et al.2005, Schneider and Wasel 2000) where moose populations increase closer to settlements. However that pattern may reflect predator avoidance behavior by moose from wolves and grizzly bears, which avoid human development (Maier et al. 2005, Weaver et al. 1996). In southern New England, black bears (*Ursus americanus*), the major predator of moose (Ballard and Van Ballenberghe 1997), are typically inactive in winter and are generally not deterred by residential development (Fecske et al. 2002, CT DEP unpublished data).

Swamps

My results suggest that swamps are an important moose habitat, perhaps because of their combination of dense (often coniferous) shade, high shrub density, and topographic setting (Thompson and Sorenson 2000). These attributes provide a concentrated food source and thermoregulation benefits. Heavy browse on shrubs and bark-stripping of sapling and pole-sized red maples was common in (though not exclusive to) swamps. Bark-stripping can kill saplings and weakens pole-size trees trees by making them more vulnerable to windthrow and insect and fungal invaders (Scharf and Hirth 2000). Local declines in red maple trees could lead to more open wetland

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Browse intensity declined with increasing proximity to human development especially in the Ware River Watershed where the northern forests are interspersed with residential development and considerably less heavily browsed than areas where development is prohibited. This result contrasted with studies in Alberta and Alaska (Maier et al.2005, Schneider and Wasel 2000) where moose populations increase closer to settlements. However that pattern may reflect predator avoidance behavior by moose from wolves and grizzly bears, which avoid human development (Maier et al. 2005, Weaver et al. 1996). In southern New England, black bears (*Ursus americanus*), the major predator of moose (Ballard and Van Ballenberghe 1997), are typically inactive in winter and are generally not deterred by residential development (Fecske et al. 2002, CT DEP unpublished data).

Swamps

My results suggest that swamps are an important moose habitat, perhaps because of their combination of dense (often coniferous) shade, high shrub density, and topographic setting (Thompson and Sorenson 2000). These attributes provide a concentrated food source and thermoregulation benefits. Heavy browse on shrubs and bark-stripping of sapling and pole-sized red maples was common in (though not exclusive to) swamps. Bark-stripping can kill saplings and weakens pole-size trees trees by making them more vulnerable to windthrow and insect and fungal invaders (Scharf and Hirth 2000). Local declines in red maple trees could lead to more open wetland forests and perhaps offset the proliferation of red maple in southern New England forests to some degree (Hall et al. 2002).

Interestingly, wetland forests including floodplains were not a significant predictor of moose browse intensity. Floodplain forests were infrequently browsed, contradicting a sizeable literature that rates floodplain riparian areas as prime moose habitat (Peek 1997, Degraaf and Yamasaki 2001). Terrace floodplain forests along small rivers in central Massachusetts are flooded irregularly (Kearsley 1999) and thus don't produce or sustain the young growth found in large, more heavily scoured floodplain communities. Shrub layers of terrace floodplain forests in my study area range from very sparse to well developed and contain a much higher proportion of exotic species such as European buckthorn (*Rhamnus frangula*) than swamps. Buckthorn was not browsed by moose, perhaps contributing to less foraging at these sites.

Landscape Scale Browse Patterns

Comparisons of the two watersheds indicate more intensive browse at the Ware River, although the categorical variable "landscape" was not a significant correlate in the multiple regression analysis. In comparison to Quabbin, Ware River has higher average elevations, greater conifer cover, and a larger proportion and total area of wetlands including swamps (MassGIS, USGS, MDC GIS layers). Importantly, harvesting at Ware River involves larger clearcuts (D. Beard pers. comm.) which may attract more intense and prolonged browsing (Faison pers. obs). The greater extent of neighboring human settlement may counteract these effects to some degree. A final difference between the two study areas is Quabbin's long history of high deer densities before 1991, which may have reduced the diversity and quality of regeneration in this watershed and thereby slowed moose population increases.

Moose and white-tailed deer

The interactions between deer and moose were investigated because the highest estimate of deer densities in Quabbin (4.8-5.6 per km^2) (McDonald et al. unpublished manuscript) match threshold levels associated with moose declines in other regions of the Northeast (Lankester and Samuel 1997). The observed lack of correlation between browse intensity and deer densities suggest that deer at these numbers are not currently influencing moose foraging in Central Massachusetts. The data are temporally mismatched, however, because the deer densities are extrapolations from deer harvest data from 2001, while the browse surveys probably reflect moose foraging from the winter of 2004-2005. Nevertheless, deer densities are believed to have changed little over the past 10 years (McDonald et al. unpublished manuscript). The data do not address the potential for different shorter-term (e.g. diurnal or seasonal) temporal use of the same habitats (Lankester and Samuel 1997).

Because white-tailed deer densities were once extremely high in Quabbin and caused structural changes to the forest (Healy 1997), it is important to discuss whether moose are functionally similar to an equivalent biomass of deer in terms of their impacts to temperate forests. Similarities exist between the two species, as studies have shown that winter browsing by deer has suppressed hemlock regeneration (Anderson and Loucks 1979, Frelich and Lorimer 1985). Differences between the animals include a higher dietary proportion of and impact to forest herbaceous plants by deer (cf. McGraw and Furedi 2005, Renecker and Schwartz 1997). In turn, moose snap and kill seedlings and saplings and strip bark from trees to a much greater extent than deer, which can lead to greater reductions in tree height and density (Crete et al. 2000). Finally, the height of moose requires young trees to grow over a meter higher to avoid being browsed than when in the presence of white-tailed deer (Curtis and Sullivan 2001, Renecker and Schwartz 1997), rendering trees vulnerable to browse suppression for a longer time.

Conclusions

The re-wilding of southern New England with its largest Holocene herbivore after a 200 year absence will undoubtedly change this temperate forest ecosystem in measurable ways in the coming decades. Current conditions -- with no wolves or human hunters and a widespread disturbance (forest harvesting) providing abundant browse -- have no historical analog and provide a setting for moose to reach greater numbers than perhaps at any time previously. Indeed, moose densities may be at least as high as they were in pre-settlement times, despite cooler temperatures associated with the Little Ice Age of that earlier period. At current population densities, winter moose foraging occurs in remote areas of higher elevations that have abundant swamps and recent and intensive forest harvests. In areas that support high moose densities, selective and sustained browsing, particularly in regenerating harvests, could promote less favored species like white pine at the expense of hardwoods and hemlock. Moose selection of intensive forest harvests in a predator-depleted landscape indicates that returning megafauna can interact with novel human conditions and disturbances and therefore impact ecosystems in different ways than before. Nevertheless, long-term effects of mammalian herbivores on plant communities are often complex and difficult to predict (Thompson and Curran 1993, Augustine and McNaughton 1998); so inevitable uncertainty accompanies these predictions. Other uncertainties exist regarding future moose viability in southern New England. The ongoing expansion of human settlement and rise in global temperatures could eventually force this heat-intolerant herbivore back to more northern areas.

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Appendix A. Correlation matrix of explanatory variables. Binary variables (swamps, hilltop, wetland, and landscape) not included. Values significantly different from 0 (P<0.05) when analyzed individually are marked by an asterisk. Values significant when Bonferroni adjustment applied (R≥0.28; P<0.0005) are in bold type with asterisk

	Lat	Ele	H2O	shrub	conifer	Red maple	Sugar maple	Hem	Spruce	oak	pine	Harvest
Latitude												
Elevation	.11											
Distance to water	-.07	.20*										
Tall shrub density	.09	-.17*	-.25*									
Distance to Conifer cover	-.24*	.08	.24*	-.21*								
Red maple relative basal area	-.02	.09	-.04	**.32***	-.13							
Sugar maple relative basal area	-.01	.08	-.03	-.15	.08	-.24*						
Hemlock relative basal area	.14	-.12	-.11	-.17*	-.18*	-.19*	-.17*					
Spruce relative basal area	.10	-.01	-.23*	.26*	-.14	-.05	-.08	.05				
Oak relative basal area	-.13	-.06	.23*	-.19*	**.28***	-.26*	-.25*	-.00	-.17*			
White pine relative basal area	.08	-.06	-.00	-.03	-.10	**-.31***	-.24	-.13	-.02	-.14		
Harvest intensity	-.13	.05	.01	-.13	.06	-.11	.02	-.00	-.11	.02	.12	
Distance to development	-.21*	-.03	.09	-.00	.13	.05	.01	-.04	.01	.09	-.14	-.01

Appendix B. Plant groups and plant taxa (all size classes combined) browsed by moose at the 95 sites where browse was recorded. Taxa avoided by moose also included. Asterisks denote taxa that occurred in at least 10 different sites. Taxa in bold type have not been previously documented to be browsed by moose (Renecker and Schwartz 1997)

Plant group/Species	**Stems Available**	**Browsed**	**Unbrowsed**	**Percentage**
Hardwoods	1085	381	704	35
Conifers	619	144	475	23
Seedlings	632	193	439	31
Saplings	857	230	627	27
Overstory Trees (>20 cm DBH)	65	33	32	51
Tall shrubs	342	121	221	35
Hemlock (*Tsuga canadensis*)*	151	75	76	50
Red maple (*Acer rubrum*)*	367	178	189	49
Witch hazel (*Hamamelis virginiana*)*	27	12	15	44
Gray birch (*Betula populifolia*)*	18	8	10	44
Winterberry (*Ilex verticillata*)*	112	48	64	43
Black cherry (*Prunus serotina*)*	108	43	65	40
Yellow birch (*Betula allegheniensis*)*	47	18	29	38
High bush blueberry (*Vaccinium corymbosum*)*	65	21	44	32
Chestnut (*Castanea dentata*)*	25	8	17	32
Red/black oak (*Quercus rubra/velutina*)*	86	21	65	24
White oak (*Quercus alba*)	17	6	11	35
Black birch (*Betula lenta*)*	265	76	189	29

Plant group/Species	**Stems Available**	**Browsed**	**Unbrowsed**	**Percentage**
Sugar maple (*Acer saccharum*)*	59	13	46	22
White pine (*Pinus strobus*)*	482	67	415	14
White ash (*Fraxinus americana*)*	40	2	38	5
Ironwood (*Carpinus caroliniana*)	54	13	42	24
American beech (*Fagus grandifolia*)	11	4	7	36
Balsam fir (*Abies balsamea*)	11	6	5	55
American hazelnut (*Corylus americana*)	15	5	10	33
Alternate-leaved dogwood (*Cornus alternifolia*)	1	1	1	100
Arrow-wood (*Viburnum dentatum*)	28	13	15	46
Black chokeberry (*Aronia melanocarpa*)	2	1	1	50
American elm (Ulmus americana)	8	1	7	13
Hop hornbeam (*Ostrya virginiana*)	12	8	4	67
Lyonia ligustrina	12	3	9	25
Mountain holly (*Nemopanthus mucronata*)	4	4	0	100
Mountain laurel (*Kalmia latifolia*)	14	1	13	7
Wild raisin (*Viburnum cassinoides*)	6	6	0	100
Hickory (*Carya* spp.)	13	1	12	8
Poison sumac (*Toxicodendron vernix*)	4	4	0	100
Quaking aspen (*Populus tremuloides*)	9	9	0	100
Shadbush (*Amelanchier* spp.)	12	3	9	25
Striped maple (*Acer pensylvanicum*)	9	5	4	56
Swamp dogwood (*Cornus amomum*)	3	1	2	33

Plant group/Species	**Stems Available**	**Browsed**	**Unbrowsed**	**Percentage**
Staghorn sumac (*Rhus typhina*) *browse observed outside of plot*	na	na	na	na
Alder (Alnus spp.)	4	0	4	0
Azalea (*Rhododendron* spp.)	3	0	3	0
Oriental bittersweet (*Celastrus orbiculatus*)	10	0	10	0
Black ash (*Fraxinus nigra*)	1	0	1	0
Black raspberry/blackberry (*Rubus* spp.)	16	0	16	0
Chokecherry (*Prunus virginiana*)	6	0	6	0
European buckthorn (*Rhamnus cathartica*)	33	0	33	0
Grape (*Vitis* spp.)	9	0	9	0
Hawthorn (*Cretagous* spp.)	6	0	6	0
Honeysuckle (*Lonicera* spp.)	5	0	5	0
Maple-leaved viburnum (*Viburnum acerifolium*)	1	0	1	0
Norway spruce (*Picea abies*)	3	0	3	0
Red pine (*Pinus resinosa*)	1	0	1	0
Red spruce (*Picea rubens)**	16	0	15	0
Spicebush (*Lindera benzoin*)	1	0	1	0
Virginia creeper (*Parthenocissus quinquefolia*)	1	0	1	0

Appendix C. Proportions of tree (saplings and poles) and shrub species bark-stripped at the 95 sites where browse was recorded. Asterisks denote species that occurred in at least 10 different sites.

Species	N	Stripped	Percentage
Red maple (Acer rubrum)*	477	49	10
Witch hazel*	31	2	6
Chestnut	19	2	11
Hemlock*	154	1	1

Appendix D. Proportion of seedlings and sapling species snapped by moose at the 95 sites where browse was recorded. Asterisks denote species that occurred in at least 10 different sites.

Species	N	Snapped	Percentage
Gray birch	17	3	18
Red maple*	276	3	1
Black cherry*	120	2	2
Hemlock*	61	1	2
Quaking aspen	9	3	33
Red oak*	52	2	4
Striped maple	11	2	18

Appendix E. Natural history observations by the author.

1. Moose beds observed in open patches of regenerating harvests surrounded by sapling white pines. These sites probably offer lateral cover and, being open-canopied, a cool microclimate at night.
2. Moose beds observed on sphagnum moss in coniferous swamps.
3. In the fall, heavily and recently trampled vegetation observed in regenerating harvests concealed by conifer saplings or thick shrub cover. Trampling had central area with circular patterns on opposite sides. Bull moose may have used these open harvests to square off during the rut.
4. In an old field succeeding to woodland at Ware River, staghorn sumac (*Rhus hirta*) was browsed extremely heavily by moose.
5. Almost all white pine browsed by moose were the leaders of seedling and saplings
6. Hemlock was browsed particularly hard when it occurred as a single individual or in low densities.
7. No exotic species were observed to be browsed by moose in the plots where they occurred. Light browse was observed on buckthorn (*Rhamnus* spp.) in one severely browsed regenerating patch cut.
8. Moose appeared to use riparian forests more as corridors than as feeding sites.
9. Moose pellet piles were not well correlated with browse intensity.
10. Moose observed during field season, 2005:
    a. Male walking through conifer swamp near Gate 35 in Quabbin (September).
    b. Female and calf running through conifer swamp at Ware River (August).
    c. Female foraging in harvested patch on the Prescott Peninsula, Quabbin (July).

d. Female running through harvested area in Hardwick zone of Quabbin Reservation (June)

e. Individual (sex unknown) foraging in perched red maple swamp in Pelham zone of Quabbin Reservation (July).