

MOOSE HABITAT IN MASSACHUSETTS: ASSESSING USE AT THE SOUTHERN EDGE OF THE RANGE

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ABSTRACT: Moose (*Alces alces*) have recently re-occupied a portion of their range in the temperate deciduous forest of the northeastern United States after a more than 200 year absence. In southern New England, moose are exposed to a variety of forest types, increasing development, and higher ambient temperatures as compared to other parts of their geographic range. Additionally, large-scale disturbances that shape forest structure and expansive naturally occurring shrub-willow communities used commonly elsewhere are lacking. We used utilization distributions to determine third order habitat selection (selection within the home range) of GPS-collared moose. In central Massachusetts, forests regenerating from logging were the most heavily used cover type in all seasons (48 - 63% of core area use). Habitat use of moose in western Massachusetts varied more seasonally, with regenerating forests used most heavily in summer and fall (57 and 46%, respectively), conifer and mixed forests in winter (47 - 65%), and deciduous forests in spring (41%). This difference in habitat selection reflected the transition from northern forest types to more southern forest types across the state. The intensive use of patches of regenerating forest emphasizes the importance of sustainable forest harvesting to moose. This study provides the first assessment of habitat requirements in this southern portion of moose range and provides insights into re-establishment of moose in unoccupied portions of its historic range in New York and Pennsylvania.

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Moose (*Alces alces*) have recently recolonized a portion of their historic range in the temperate deciduous forest of southern New England after more than 200 years absence (Vecellio et al. 1993, Wattles and DeStefano 2011). This environment is unique in moose range and provides a number of potential challenges, including forest types that differ from most of the geographic range (Westveldt et al. 1956, DeGraaf and Yamasaki 2001, Franzmann and Schwartz 2007), a thermal environment that could

reduce fitness and survival (Renecker and Hudson 1986, Boose 2001, Murray et al. 2006, Lenarz et al. 2009, 2010), and high levels of human development (U. S. Census Bureau 2000, DeStefano et al. 2005).

Habitat use and diet have been studied throughout much of moose range (Franzmann and Schwartz 2007), including elsewhere in the northeastern United States (Crossley and Gilbert 1983, Leptich and Gilbert 1989, Garner and Porter 1990, Miller and Litvaitis 1992, Thompson et al. 1995,

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Scarpitti et al. 2005, Scarpitti 2006). However, similar information has been lacking in the transitional forests of southern New England. The recolonization of southern New England saw moose push the southern extent of their range from spruce-fir and northern hardwood forests into transitional and more southerly forest types, which lack many of the plant species preferred by moose further north. Massachusetts provides a unique environment to examine the effects of this transition in use of forest types and habitat selection over a relatively small area. The objectives of this study were to 1) determine how moose use the temperate deciduous forest of southern New England, 2) compare habitat use among seasons, and 3) assess whether suitable habitat exists to support long-term occupation of southern New England.

STUDY AREA

The study area was located in central and western Massachusetts, USA (Fig. 1). Topography is dominated by glaciated hills underlain by shallow bedrock. Glacial activity created abundant small stream valleys, lakes, ponds, and wetlands whose size and nature vary with beaver (*Castor canadensis*) activity. The central and western sections of the study area are separated by the Connecticut River Valley which runs N-S through west-central Massachusetts. Elevation ranges from 100 m above sea level in the Connecticut River Valley to 425 m in the hills of central Massachusetts, and 850 m in the Berkshire Hills of western Massachusetts.

The western two-thirds of Massachusetts was >80% mixed deciduous, second- or multiple-growth forest, much of it resulting from regeneration of farm fields abandoned

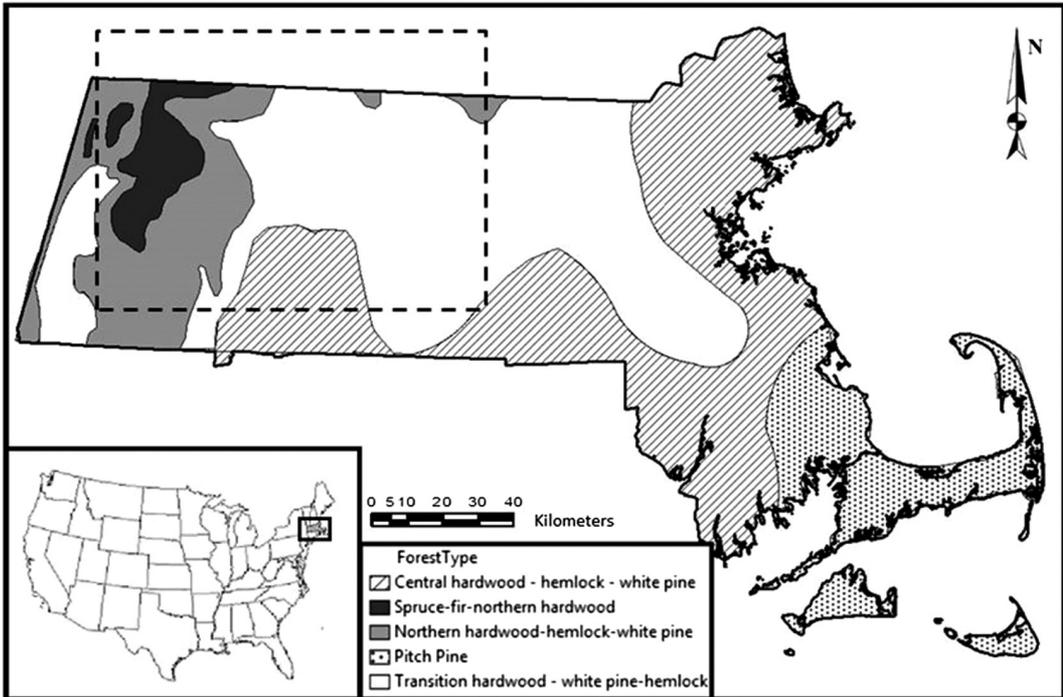


Fig. 1. Area used to study moose-habitat relationships in northeastern USA, specifically west-central Massachusetts depicted in blow-up with dashed line, and bordered by southern Vermont and New Hampshire. Figure also depicts the forest types of Massachusetts (after Westveldt et al. 1956 and DeGraaf and Yamasaki 2000).

in the mid-to-late 1800s (Hall et al. 2002). With the exception of wetlands and small-scale logging, the undeveloped portion of the Massachusetts landscape was nearly 100% closed canopy mixed-coniferous-deciduous forest. Massachusetts represents a forest transition zone, where forests shift from those common in northern New England to more southern forest types.

Moose transition across 4 forest types in Massachusetts, including spruce-fir-northern hardwoods, northern hardwoods-hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*), transition hardwoods-white pine-hemlock, and central hardwoods-hemlock-white pine (Fig. 1). The spruce-fir-northern hardwoods type is dominated by spruce (*Picea* spp.), balsam fir (*Abies balsamea*), American beech (*Fagus grandifolia*), birch (*Betula* spp.), trembling aspen (*Populus tremuloides*), eastern hemlock, and maple (*Acer* spp.). In the northern hardwoods forest, white pine and hemlock largely replace spruce and fir. Transition hardwoods-white pine-hemlock forests contain most of the species in the northern hardwoods type; in addition, oaks (*Quercus* spp.) and hickories (*Carya* spp.) become increasingly common. In the central hardwoods-hemlock-white pine forest, beech, sugar maple (*A. saccharum*), and yellow birch (*B. alleghaniensis*) are rare, replaced by oaks and hickories. Transitions between forest types can be gradual or distinct depending on localized physiography, climate, bedrock, topography, land-use history, and soil conditions, resulting in a patchwork of forest types and species groups (Westveldt et al. 1956, DeGraaf and Yamasaki 2001).

Early successional habitat was created primarily through timber harvest practices, and occasionally through wind and other weather events. From 1984 to 2000, about 1.5% of the forest was logged annually, consisting of small (mean = 16.5 ha) cuts of moderate intensity (removal of 27% of

timber volume) widely distributed on the landscape (Kittredge et al. 2003, McDonald et al. 2006). The pattern of forest harvest, glaciation, and transitional forest types provided a patchy mosaic of well interspersed forest types, age classes, and wetlands.

July was the warmest month when mean daily temperature was 21.1 °C, and January the coldest when mean daily temperature was -6.1 °C. Mean annual precipitation was 107 cm in central areas and 124 cm in western areas, with all months receiving 7–11 cm and 8–12 cm, respectively (The Weather Channel 2011a, 2011b). The average date of last frost in the region was 15 May; the average day of first frost was 1 October and 15 September in central and western areas, respectively (DeGraaf and Yamasaki 2001). Maximum snow depth was typically greater in western Massachusetts than central areas and reaches depth in both areas (50–70 cm) that can restrict moose movement (Coady 1974).

METHODS

Study Animals and GPS Telemetry

Adult (>1 yr old) moose were captured by locating, stalking, and darting them from the ground in state forests, wildlife management areas, and other conservation areas between March 2006 and November 2009. Moose were immobilized using either 5 mL of 300 mg/ml or 3 mL of 450 mg/mL xylazine hydrochloride (Congaree Veterinary Pharmacy, Cayce, South Carolina, USA; mention of trade names does not imply endorsement by the U. S. Government) administered from a 3 or 5 cc Type C Pneu-dart dart (Pneudart, Inc., Williamport, Pennsylvania, USA). Tolazolene (100 mg/mL) at a dosage of 1.0 mg/kg was used as an antagonist. Moose were fitted with GPS collars; either ATS G2000 series (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) or Telonics TWG-3790 GPS collars (Telonics, Inc., Mesa, Arizona, USA).

We programmed the collars to attempt a GPS fix as frequently as possible while allowing the battery life to extend for at least 1 year; depending on the collar, a GPS fix was attempted every 135, 75, or 45 min. Collars were equipped with very high frequency (VHF) transmitters, mortality sensors, and release mechanisms that opened the collars either at a low battery state or a preprogrammed date. Capture and handling procedures were approved by the University of Massachusetts Institutional Animal Care and Use Committee, protocol numbers 25-02-15, 28-02-16, and 211-02-01.

Seasons

We defined the length and timing of seasons based on several ecological factors including timing of the growing season of vegetation, weather (including temperature and snow conditions), and the moose reproductive cycle (Table 1). The transition between seasons can vary by several days to several weeks depending on weather conditions and other factors. If movements were identified in the location data for an animal

that obviously demonstrated a change in season (e.g., a large increase in movements at the end of the winter when snow had melted, or at the end of summer indicating the beginning of rutting behavior), the data were truncated at that point and included in the following season.

Habitat Availability and Core Area Habitat Use

We compared vegetation and land cover types in the home range cores of moose to that available in larger MCP home ranges (third-order habitat selection; Johnson 1980). We used a fixed kernel density estimator (KDE) (Worton 1989) and the Kernel Density Estimation tool in HRT: Home Range Tools for ArcGIS (Rogers et al. 2007) to calculate utilization distributions (UD). We then used the Create Minimum Convex Polygons tool in Hawth's Tools (Beyers 2006) to calculate 100% minimum convex polygon (MCP) home ranges (Mohr 1947). All Geographic Information System (GIS) work was performed in ArcGIS 9.3 (ESRI 2008).

Table 1. Seasons used for calculating home-range, movements, and core-area habitat analyses.

Season	Dates	Vegetation/ Browse	Temperature ^a	Movement	Season length (d)
Spring	16 April – 31 May	Growing season; bud-break-leaf out	Cool-Hot	Not snow restricted, potentially temperature restricted	46
Calving (females)	8–13 May – 15 June	Growing season; bud-break-leaf out	Cool-Hot	Restricted by newborn calf	30
Summer	1 June – 30 Aug	Growing season; full leaf out	Hot	Restricted by temperature	92
Fall	1 Sept – 31 Oct	Leaf out to leaf off	Hot-Cool	Rut and temperature influenced	61
Early Winter	1 Nov – 31 Dec	Dormant season; woody/evergreen	Warm-Cold	Not snow restricted, potentially metabolism restricted	61
Late Winter	1 Jan – 15 April	Dormant season; woody/evergreen	Cold-Warm	Potentially snow and metabolism restricted	107

^aTemperature ranges describing typical temperatures experienced during a season; Cold ≤0°C, Cool >0°C and <14°C, Warm ≥14°C and <20°C, Hot ≥20 °C.

The kernel bandwidth or smoothing factor (h) is known to have the greatest effect on UD (Worton 1989). A large h over-smooths the data, resulting in a more biased UD that encompasses unused habitats, while a small h under-smooths the data, resulting in a fragmented UD (Fieberg 2007). There is lack of agreement on the best method for calculating h (Powell 2000, Hemson et al. 2005, Gitzen et al. 2006, Fieberg 2007, Kie et al. 2010); therefore, we used 2 values (80 m and 30 m) of h to calculate UDs. We used the 50-percent isopleth of the 80 m UD to identify home range cores. However, the 80 m bandwidth still resulted in over-smoothed UDs with large buffers around GPS locations that incorporated unused habitat. As a result we used a second h value of 30 m, based on the median distance between GPS locations for our most intensively sampled animals, approximating within-patch movement of the animals. The resulting UDs incorporated little unused habitat and were used to assess habitat use within the core areas calculated with the 80 m h .

We classified habitats into 8 categories: coniferous forest (mostly coniferous with minimal deciduous component), deciduous forest (mostly deciduous with minimal coniferous component), mixed forest (mixed deciduous and coniferous), regenerating forest (logged areas <20 years old and power-line right-of-ways), wooded wetlands (conifer, mixed, and deciduous wooded wetlands), other wetlands (grassy fens, shrub swamps, bogs, deep wetlands, and open water), open (e.g., fields and meadows), and developed. We set the age restriction of regenerating forest at 20 years because, while logged areas >20 years may still provide browse, these stands more closely resembled mature forest. In addition, older harvests were difficult to distinguish or map accurately. Open and developed were absent

from almost all core area habitat use and were later dropped from the analysis.

We manually digitized cover and land use within the cores in ArcGIS 9.3 (ESRI 2008) using a compilation of available GIS base-layers from the Massachusetts Office of Geographic Information (MassGIS; MassGIS 2011) and other sources, including 2005 and 2009 orthophotos, Department of Environmental Protection wetland layers, forest harvest information from the Massachusetts Department of Conservation and Recreation (DCR) and Harvard Forest (McDonald et al. 2006), 2003 and 2009 National Agricultural Imagery Program (NAIP) satellite imagery, and mid-1990s black and white orthophotos, as well as state wetland layers for Vermont and New Hampshire.

We assessed habitat availability within the home range by generating sets of 250 random points within 100% annual MCP home ranges using the Generate Random Points tool in Hawth's Tools (Beyers 2006, Wattles 2011) and manually classifying cover and land use. We calculated use:availability ratios by comparing cover and land use within 30 m UD core areas (used) to MCP home ranges (available) (Aebischer et al. 1993). Use:availability ratios >1 indicated a cover type was used more than available; a ratio <1 indicated use was less than available. Calving sites were identified based on large decreases in daily movement of cows followed by a concentration of GPS locations during the calving season (May–June) (Poole et al. 2007).

Analyses

We used analysis of variance (ANOVA) to analyze the differences in habitat availability, core area habitat use, and use:availability ratios within and between sexes, seasons, and portions of the study area. We used type III ANOVA to account for unequal sample sizes among groups and seasons. We performed pairwise comparisons using

Tukey's contrasts with adjusted *P*-values using the single-step method. Significance level for all analyses was set at 0.05. We used R, version 2.12.2 (R Development Core Team 2005) for all statistical analyses.

RESULTS

Capture and Deployment of GPS Collars

We deployed GPS collars on 26 adult moose (7 females and 19 males); 5 were excluded due to mortality, suspected infection with brainworm (*Parelaphostrongylus tenuis*), or collar failure. Data analysis included 5 females and 8 males in central and 8 males in western Massachusetts. Nine moose were recaptured and recollared when

the batteries in their initial GPS collars ran low. We obtained 127,408 locations from the 21 moose with an overall fix rate of 85%. Seasonal data for any animal were included in the analyses only if data were obtained across the entire season. The median number of locations per animal per season ranged from 402 in spring to 1,015 in late winter. The minimum number of locations was 281 for one animal in spring.

Home Range Core Area Habitat Use

Habitat use within seasons. Regenerating forest was used more than all other cover types by both central males and females during all seasons (proportion of use 0.48 to

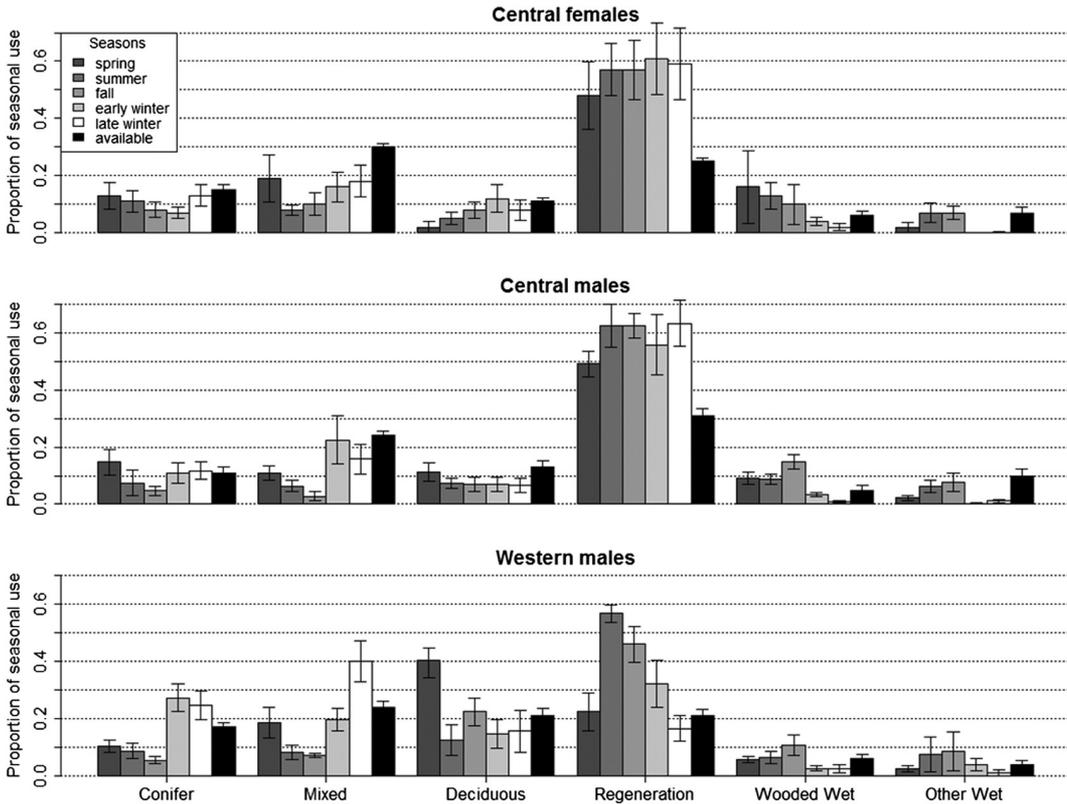


Fig. 2. Mean proportional seasonal core area habitat use for female (n = 5, 5, 4, 5, and 5 individuals for spring, summer, fall, early winter, and late winter, respectively) and male (n = 7, 7, 7, 6, and 7 individuals for spring, summer, fall, early winter, and late winter, respectively) moose in central Massachusetts and male moose in western Massachusetts (n = 7, 6, 4, 8, and 7 individuals for spring, summer, fall, early winter, and late winter, respectively). Error bars represent standard errors of the means.

Table 2. *P*-values for ANOVA of use:availability ratios. Dark gray indicates use:availability >1, light gray <1, and white use not significantly different than availability.

	Spring	Summer	Fall	Early Winter	Late Winter
Females					
Coniferous	0.688	0.329	0.066	0.027	0.611
Mixed	0.219	<0.001	0.001	0.030	0.070
Deciduous	0.008	0.045	0.228	0.368	0.561
Regenerating	0.089	0.008	0.010	0.021	0.028
Wooded Wetland	0.445	0.213	0.523	0.113	0.090
Other Wetland	0.061	0.958	0.956	0.004	0.006
Central Males					
Coniferous	0.508	0.458	0.035	0.940	0.898
Mixed	<0.001	<0.001	<0.001	0.786	0.145
Deciduous	0.687	0.059	0.088	0.072	0.066
Regenerating	0.004	0.002	<0.001	0.039	0.003
Wooded Wetland	0.077	0.063	0.002	0.358	0.004
Other Wetland	0.007	0.190	0.482	0.001	0.045
Western Males					
Coniferous	0.037	0.024	0.002	0.089	0.188
Mixed	0.369	<0.001	0.165	0.393	0.053
Deciduous	0.014	0.165	0.809	0.300	0.505
Regenerating	0.885	<0.001	0.083	0.249	0.360
Wooded Wetland	0.677	0.988	0.181	0.027	0.049
Other Wetland	0.139	0.609	0.475	0.722	0.019

0.63; $P \leq 0.006$), with the exception of wooded wetlands, mixed forest, and conifer forests during spring by females (Fig. 2). No other differences in seasonal core area habitat use were significant for central males or females. Both central males and females showed selection for regenerating forest during all seasons (Table 2), except for females during spring. Central males also showed selection for wooded wetlands during fall. All other habitat types were either used in proportion to or less than their availability. The lack of selection of regenerating forests by females in spring was likely because calving areas dominated female spring habitat use; calving sites varied among individuals and included wooded wetlands, mature

mixed and conifer-dominated mixed stands, and mixed and conifer shelter cuts.

The importance of vegetative cover type varied with season for western males (Table 2, Fig. 2), that selected for deciduous forest and used it (proportional use = 0.41) more than all other habitat types except regenerating forest during spring ($P \leq 0.03$). Regenerating forest (0.22) was also used more than other wetlands at this time of year ($P = 0.03$). During summer (0.57) and fall (0.46) regenerating forest use was greater than all other habitat types ($P \leq 0.02$); however, it was used more than its availability only during summer. No other habitat types were used more than their availability at any other time of year. Forest

types with a conifer component (mixed and coniferous forest) combined to be most used in early (0.47) and late winter (0.65). High use of regenerating forest continued in early winter (0.32).

Habitat use among seasons. There were no differences in the use of various vegetative cover types by females among seasons. Central males used more mixed forest in early winter than fall ($P = 0.046$). Central males used wooded wetlands more during fall than early and late winter ($P < 0.001$), and more during both spring and summer than in late winter ($P \leq 0.02$). Western males used less conifer forest in their home range cores during spring, summer, and fall than in early winter ($P \leq 0.03$), and less in fall than late winter ($P \leq 0.04$). Similarly, they used more mixed forest in late winter cores than all other seasons, but only significantly more in fall ($P \leq 0.01$). Western males use regenerating forests more during summer than spring ($P = 0.02$) or late winter ($P = 0.01$), while use of deciduous forest was greater during spring than summer and early or late winter ($P \leq 0.04$). Wooded wetland use was greater during fall than early and later winter ($P \leq 0.03$).

Habitat use based on gender and region. There were no differences in seasonal core area habitat use between central males and females. However, western males used deciduous forest more than central males or females during spring and fall ($P \leq 0.01$), and more coniferous forest during early winter ($P \leq 0.02$). Western males also used more mixed forest than central males during late winter ($P = 0.03$), but less regenerating forest ($P = 0.04$) than central males during spring, and less regenerating forest than either central males or females in late winter ($P \leq 0.01$).

DISCUSSION

Not all areas within a home range hold equal importance to the animal. If food and other resources are unevenly distributed, areas of higher densities of critical resources should be more important than areas with lower levels of that resource (Powell 2000). If animals focus their use in some portion of the home range where resources are concentrated, those areas represent centers of activity or cores of the home range (Hayne 1949, Kaufmann 1962, Samuel et al. 1985, Powell 2000). Due to the concentrated use of these areas, home range cores may be critically important to an individual's survival and reproductive success. Identifying home range core areas and core area habitat can provide important insights into the ecology of a species and its survival strategies. This is particularly important for managers in southern New England, where moose have only recently re-established after many decades of absence and where habitat differs from much of the rest of their geographic range.

The typical annual pattern of habitat use by moose reflects the seasonal availability of resources (Peek 2007). Sites that optimize forage quantity and quality vary by forest type and season and are a main driver of the vegetative cover types that moose select (Telfer 1988, Westworth et al. 1989, McCracken et al. 1997, Poole and Stuart-Smith 2005, Peek 2007). As a result, habitat use follows a familiar pattern across their geographic range (Peek 2007). For example, moose in our study were extremely reliant on young, regenerating forest for browse (Phillips et al. 1973, Pierce and Peek 1984, Bangs et al. 1985, McCracken et al. 1997, Poole and Stuart-Smith 2005, Peek 2007, Gillingham and Parker 2008); used wetlands for thermal cover (Renecker and Hudson 1986) and some summer forage (Ritcey and Verbeek 1969, Jordan et al. 1973, Crossley

and Gilbert 1983, Morris 2002); browsed conifers such as balsam fir (where available) and hemlock in winter (Crossley and Gilbert 1983, Thompson et al. 1995); and used conifers as cover during warm periods (Schwab and Pitt 1991, Dussault et al. 2004) and periods of deep snow (Peek et al. 1976, Monthey 1984, Thompson et al. 1995).

However, we found large differences in the availability and distribution of some vegetative cover types compared to the rest of the species range, which resulted in differences in habitat selection. Probably the most important difference was the amount and distribution of early successional forest habitat and the processes that create these habitats. While this cover type was heavily used by moose, large disturbances that create it – either natural (fire, wind, insects) or human-caused (logging) – are rare and becoming rarer in southern New England. The amount and distribution of timber harvesting activities is minimal as compared to many other regions, and large-scale natural processes such as flooded river deltas, sup-alpine and riparian shrub communities, and avalanche corridors do not exist. In addition, some key woody species such as willows (*Salix* spp.), aspen, mountain-ash (*Sorbus americana*), and other shade-intolerant species, all of which provide high quality browse for moose in more northern regions, are not abundant in southern New England. With the exception of wetlands and small-scale logging, the undeveloped portion of the Massachusetts landscape is nearly 100% closed canopy mixed-coniferous-deciduous forest. As a result, moose use the various cover types of closed canopy forest, small wetlands, and patches of young forest created by logging. Additionally, while wetlands that supported aquatic vegetation were used throughout spring, summer, and fall, and these sites likely provided critical nutrients, their importance as feeding sites was relatively low compared

to regenerating forests in our study area and to wetlands elsewhere in moose range (Jordan et al. 1973, Crossley and Gilbert 1983, Ritcey and Verbeek 1989, Morris 2002). Similarly, while roadside salt licks are commonly used by moose in northern New Hampshire (Miller and Litvaitis 1992, Scarpitti et al. 2005), we saw no indication of the use of roadside wetlands that would indicate their use as salt licks.

We also saw clear differences in forest cover use between central and western Massachusetts, and by extension between the forest types of southern and northern New England. The most important factor was likely the transition across the state from spruce-fir-northern hardwoods and northern hardwoods-hemlock-white pine forest to the transition hardwood-white pine-hemlock and central hardwood-hemlock-white pine forest types, and the associated changes in plant communities and structure. The forests in the Berkshire Mountains of western Massachusetts are similar to forests in southern Vermont and New Hampshire (DeGraaf and Yamasaki 2001), and use of these forests reflected many similar habitat patterns that have been reported in northern New England (Crossley and Gilbert 1983, Leptich and Gilbert 1989, Thompson et al. 1995, Scarpitti 2006).

Conifer and mixed-coniferous-deciduous stands, with balsam fir and hemlock, were important cover types during winter in western Massachusetts, as in northern New England (Crossley and Gilbert 1983, Thompson et al. 1995, Scarpitti 2006). Balsam fir occurred in the spruce-fir-northern hardwood forests at the highest elevations in western Massachusetts, but it was absent in central Massachusetts and lower elevations in western Massachusetts. With the absence of balsam fir, hemlock was the only conifer that was a large portion of the winter diet of moose; white pine was avoided (Faison et al. 2010). While the use of stands of hemlock and mixed stands with hemlock

and deciduous shrubs and saplings increased in central Massachusetts during winter, the lack of balsam fir increased reliance on high-density regenerating stands of hardwoods. Additionally, typically less restrictive snow conditions in central Massachusetts (20–60 cm in late winter) may have played a role in the increased use of regenerating stands in late winter, while deep snow (80–110 cm in late winter) in western Massachusetts may have forced moose into the shelter of spruce-fir stands.

Similarly, western males used deciduous forests more in spring and fall compared to moose in central Massachusetts. Favored deciduous species, such as hobblebush (*Viburnum lantanoides*), striped maple (*A. pennsylvanicum*), beech (early in the growing season), and aspen were less common in central Massachusetts, and the reduced availability of these key species seemed to limit use of deciduous forest in central compared to western areas.

The dominant habitat type used by moose throughout the state was regenerating forest created by logging. In central Massachusetts moose used areas of forest regeneration intensively in all seasons. While use of regenerating stands in western Massachusetts was more variable, moose still concentrated in these sites, especially during summer. Early seral stage forest stands provided a concentrated source of abundant browse during the growing season (McDonald et al. 2008), which allow moose to maximize their forage intake without moving over large areas (Belovsky 1981, Wickstrom et al. 1984). The use and selection of these sites during summer ($\geq 57\%$ of home range core areas by all groups) suggests that moose relied on regenerating forests to provide the forage required to gain weight at this critical time of year (Belovsky and Jordan 1978, Van Ballenberghe and Miquelle 1990).

The recent pattern of logging in Massachusetts appeared to be favorable to moose.

Harvest sites on state and private lands were widely distributed, with $< 2\%$ of the forested landscape logged annually (Kittredge et al. 2003, McDonald et al. 2006). This resulted in new patches of early successional habitat within a matrix of mature and maturing forest. The importance of thermal cover for moose in and around forest harvests and burns has been well documented (McNicol and Gilbert 1980, Girard and Joyal 1984, Bangs et al. 1985, Masterbrook and Cummings 1989, Thompson et al. 1995). The small size (mean = 16.5 ha) and moderate harvest intensity (27% of timber volume harvested) of forest harvest units in Massachusetts (Kittredge et al. 2003) resulted in short distance to edge, which provided both browse and cover in close proximity. Shelterwood cuts were commonly applied to harvest units, resulting in cover from solar radiation along with browse, with the added advantage that vegetation growing in shade tends to be more nutritious and has lower secondary compound levels than growth in direct sunlight (Hjeljord et al. 1990, Schwartz and Renecker 2007).

The intense use of regenerating forests is similar to habitat use in northern New England and elsewhere (Peek et al. 1976, Joyal and Scherrer 1978, Crossly and Gilbert 1983, Monthey 1984, Leptich and Gilbert 1989, Thompson et al. 1995, Scarpitti 2006). However, both Leptich and Gilbert (1989) and Miller and Litvaitis (1992) found that only females selected for cut-over areas during summer in northern New Hampshire and northern Maine, with males selecting upland hardwoods; Scarpitti (2006) found selection for regenerating stands only during winter. The high concentration of browse found in regenerating stands mimicked the permanent shrub communities used by moose in other portions of their range, including delta floodplains, tundra and sub-alpine areas, aspen parklands, and stream valley shrub communities, as well as the

transitory early successional habitats created by fire and insect outbreaks (Phillips et al. 1973, Pierce and Peek 1984, Bangs et al. 1985, McCracken et al. 1997, Poole and Stuart-Smith 2005, Peek 2007, Gillingham and Parker 2008).

The clear importance of early successional forest as foraging habitat for moose, however, should not take away from that fact that moose used a mix of cover types and age classes to meet their annual habitat needs in southern New England. Mature coniferous, mixed, and deciduous stands were seasonally important foraging sites. Additionally, moose used mature forests and a variety of wetlands as thermal shelters during periods of high temperature, and mature coniferous and mixed stands during periods of deep snow.

While moose now occupy most suitable habitat in Massachusetts and Connecticut, additional habitat may exist in unoccupied portions of its historic range in New York and Pennsylvania. Forest types transition in New York and Pennsylvania in a similar way as in Massachusetts, from spruce-fir and northern hardwood forests to transitional and central hardwood forests, and suitable habitat likely exists for moose in the forest types of southern New York and Pennsylvania. However, different state management goals (Wattles and DeStefano 2011), greater amounts of agriculture, the highly developed Mohawk River Valley, and high temperatures may prevent or slow the further expansion of moose in this region.

MANAGEMENT IMPLICATIONS

The year-round intensive use of regenerating forests by moose in Massachusetts underlies the importance of early successional forest. The recent pattern of logging that continually created new patches of young forest seemed to be favorable for moose. However, recently adopted plans by the DCR (the agency that manages the state

forest system and public watersheds in Massachusetts) that restrict or eliminate logging on some state lands could have a negative impact on moose and other wildlife that use or require early successional forest. Moose rely on these sites of high forage density to gain weight for winter and support lactation of calves. A reduction in logging would result in a loss of this cover type over time from some of the largest tracts of conservation land and would force moose to forage for lower density browse in mature forest stands. This could result in higher energy expenditures to obtain the same amount of food, which may be particularly harmful for a species living in an environment at the extremes of its temperature tolerances. That heat stress has been implicated in the recent declines in moose populations elsewhere along the southern edge of the species' range (Murray et al. 2006, Lenarz et al. 2009, 2010) demonstrates the importance of energy balance for moose living in these environments.

Management of moose habitat on a landscape scale in Massachusetts should ensure the protection of large blocks of forested habitat that support a mix of age classes and forest cover types, including mature stands of coniferous, mixed-coniferous-deciduous, and deciduous forests, patches of early successional forest, and a variety of wetlands. The mix of cover types, age classes, and wetlands that currently occur in the temperate deciduous forests of Massachusetts and southern New England appear to provide suitable habitat for long-term occupation by moose.

In general, moose are relatively widely dispersed, actively reproducing, and present at low density in almost all forest types in central and western Massachusetts. The absence of major predators and hunting undoubtedly influence the population dynamics of moose in Massachusetts. The differences in the distribution, structure, and landscape

configuration of key habitat components, along with large levels of development and a potentially thermally stressful environment will likely combine to limit the distribution and density of moose in southern New England.

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