

SPACE USE AND MOVEMENTS OF MOOSE IN MASSACHUSETTS: IMPLICATIONS FOR CONSERVATION OF LARGE MAMMALS IN A FRAGMENTED ENVIRONMENT

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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 >200 year absence. In southern New England, moose encounter different forest types, more human development, and higher temperatures than in other parts of their geographic range in North America. We analyzed seasonal minimum convex polygon home ranges, utilization distributions, movement rates, and home range composition of GPS-collared moose in Massachusetts. Seasonal home range sizes were not different for males and females and were within the range reported for low latitudes elsewhere in North America. Seasonal movement patterns reflected the seasonal changes in metabolic rate and the influence of the species' reproductive cycle and weather. Home ranges consisted almost entirely of forested habitat, included large amounts of conservation land, and had lower road densities as compared to the landscape as a whole, indicating that human development may be a limiting factor for moose in the region. The size and configuration of home ranges, seasonal movement patterns, and use relative to human development have implications for conservation of moose and other wide-ranging species in more highly developed portions of their ranges.

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An animal's home range is the area where it finds the resources it needs for survival and reproduction (Burt 1943); essentially it is a measure of spatial use for a given period of time. Different home range estimators provide different information regarding how the animal uses space, including total area, areas of intensive use, and areas that are avoided (Powell 2000, Fieberg and Börger 2012). Animals have a cognitive map of their home range which allows them to exploit areas of concentrated resources and avoid areas that impart risks or disadvantages (Powell 2000, Powell and Mitchell 2012, Spencer 2012). Thus home range size, configuration, and use can be influenced by the type, concentration, and

distribution of resources, topography and other physical features, human development, and the distribution of other animals such as mates, competitors, and predators (Powell and Mitchell 2012). Further, space use and movement patterns show seasonal changes which can be influenced by temperature and other climatic factors such as snow condition, reproductive status (Börger et al. 2006, Birkett et al. 2012), and for species that are affected by seasonal changes in forage quantity and quality like moose (*Alces alces*) and other ungulates, foraging times, ruminating times, and metabolic rates (Risenhoover 1986, Cederlund 1989). Knowledge of the size and position of an animal's home range and an individual's

movements and use of that area can provide insights into the distribution of resources and limiting factors in the environment (Powell 2000, Rettie and Messier 2000, Powell and Mitchell 2012, Spencer 2012).

In areas of high human density, development of the landscape can be a major determinant of landscape use by many wildlife species (Forman and Deblinger 2000, Lykkja et al. 2009, Kertson et al. 2011). The concentration and distribution of industries and businesses, residences, roads and other infrastructure, and even the abundance of pets can affect the availability, quality, distribution, and connectivity of wildlife habitats. This is likely true for many or most taxa, but it is especially obvious for large mammals such as moose that require extensive areas to fulfill their life history needs.

Despite beliefs that temperature (Kelsal and Telfer 1974, Renecker and Hudson 1986, Peek and Morris 1998) and human development (Vecellio et al. 1993, Peek and Morris 1998) might prevent it, moose have recently recolonized and become established in a portion of their historic range in the temperate deciduous forest of southern New England (Vecellio et al. 1993, Wattles and DeStefano 2011). This environment provides a number of potential challenges for moose, including forest types that differ from that found in most of its 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 some of the highest densities of people in the United States (DeStefano et al. 2005, U. S. Census Bureau 2010a).

Habitat use, home range, and movement of moose have been studied throughout much of its range (Franzmann and Schwartz 2007), including elsewhere in the northeastern U. S. (Leptich and Gilbert 1989, Garner and Porter 1990, Miller and Litvaitis 1992,

Thompson et al. 1995, Scarpitti et al. 2005). However, similar information has been lacking in southern New England where urban and suburban development and high road densities result in fragmentation of much of the landscape and relatively small and scattered natural areas.

Our objective was to determine how moose use the landscape in the human-dominated and developed environment of central and western Massachusetts. Specifically, we wanted to quantify the seasonal home range size, space use patterns, and movement rates of moose in this recently re-established population. It is well documented that the reproductive cycle (e.g., the rut) and seasonal changes in forage affect movement patterns (Belovsky 1981, Risenhoover 1986, Cederlund 1989, Van Ballenberghe and Miquelle 1990), and we further predicted that movements would be influenced by weather patterns not experienced by moose elsewhere. Also, due to the relatively limited number of human-moose conflicts reported in the state (Wattles and DeStefano 2011), we predicted that moose would avoid areas with high levels of human development, locate their home ranges away from people, and that home range size and configuration would be influenced by development level.

METHODS

Study Area

Our study was conducted in central and western Massachusetts, USA and adjacent portions of Vermont and New Hampshire, between 42° 9' and 42° 53' N latitude and 71° 53' and 73° 22' W longitude. 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 varies with changes in 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 in the mid-late 1800s (Hall et al. 2002). Forest types included spruce-fir-northern hardwoods, northern hardwoods-hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*), transition hardwoods-white pine-hemlock, and central hardwoods-hemlock-white pine. Transitions between forest types can be gradual or distinct depending on localized physiography, climate, bedrock, topography, and soil conditions, resulting in a patchwork of forest types and species groups (Westveldt et al. 1956, DeGraaf and Yamasaki 2001). Dominant species included spruce (*Picea* spp.), balsam fir (*Abies balsamea*), American beech (*Fagus grandifolia*), birch (*Betula* spp.), trembling aspen (*Populus tremuloides*), eastern hemlock, oaks (*Quercus* spp.), hickories (*Carya* spp.), and maples (*Acer* spp.) depending on area and forest type.

Early successional habitat was created primarily through logging, and occasionally through wind and other weather events. About 1.5% of the forest was logged annually in 1984–2000, 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 is the warmest month when mean daily temperature is 21 °C, and January the

coldest when mean daily temperature is –6 °C. Mean annual precipitation is 107 cm in central areas and 124 cm in western areas, with all months receiving 7–11 cm and 8–12 cm, respectively (DeGraaf and Yamasaki 2001). The average date of last frost in the region is 15 May; the average day of first frost is 1 October and 15 September in central and western areas, respectively (DeGraaf and Yamasaki 2001). Snow depth is typically greater in western than central areas, and depths that restrict moose movement (50–70 cm) can occur in both areas (Coady 1974).

Massachusetts is one of the most densely populated states in the U. S. (DeStefano et al. 2005; U. S. Census Bureau 2010a). Development intensity is variable throughout the state, but tends to be substantially less in the uplands compared to the valley floors (<15–35 people/km² in uplands and 35–>360/km² in valley floors outside of major urban centers; U. S. Census Bureau 2010b). Development in the uplands consists primarily of isolated homes and homes lining roadways within a matrix of forest; agricultural land and medium-to-large towns dominate the valleys. There is a dense road network throughout the area, consisting of state highways, paved, and unpaved municipal roads: 0.78 and 2.22 km of paved roads/km² and 0.76 and 1.12 km of unpaved roads/km² for uplands and valleys, respectively.

Study Animals and GPS Telemetry

We captured adult (>1 yr old) moose by opportunistically stalking and darting them from the ground 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, SC, USA; mention of trade names does not imply endorsement by the U. S. Government) administered from a 3 or 5 cc Type C Pseudart dart (Pseudart, Inc., Williamport,

PA, USA). We used Tolazolene (100 mg/ml) at a dosage of 1.0 mg/kg as an antagonist. Moose were fitted with GPS collars, either ATS G2000 series (Advanced Telemetry Systems, Inc., Isanti, MN, USA) or Telonics TWG-3790 GPS collars (Telonics, Inc., Mesa, AZ, 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 also equipped with VHF transmitters, mortality sensors, and mechanisms that released the collars either at a low battery state or a pre-programmed 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 *a priori* defined the length and timing of seasons based on several ecological factors including vegetation phenology, weather (including temperature and snow conditions), and the moose reproductive

cycle (Table 1). The transition between seasons could vary by several days to several weeks depending on weather conditions and other factors. If movements were seen in the data that obviously demonstrated a change in season (e.g., a large increase in movement at the end of the winter when snow had melted or the end of summer indicating the beginning of rutting behavior), the seasons were truncated at that point and the data were included in the following season (Fig. 1).

Home Ranges and Space Use

We used 2 methods to calculate space use by moose: minimum convex polygon (MCP) and utilization distributions (UD) by fixed kernel density estimator. We calculated 100% MCP home ranges with the Create Minimum Convex Polygons tool in Hawth's Analysis Tools (Beyers 2006) and UDs using the Kernel Density Estimation tool in HRT: Home Range Tools for ArcGIS (Rodgers et al. 2007). 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 for moose in Massachusetts, 2006–2011. Season breaks were based on phenology of vegetation, temperature, normal snow conditions, and moose reproductive activity.

Season	Dates	Vegetation/Browse	Temperature ^a	Movement moderators	Season length (d)
Spring	16 April–31 May	Growing season; bud-break-leaf out	Cool-Hot	Potentially temperature	46
Calving (females)	8–13 May–15 June	Growing season; bud-break-leaf out	Cool-Hot	Newborn calf mobility	30
Summer	1 June – 30 Aug	Growing season; full leaf out	Hot	Temperature	92
Fall	1 Sept – 31 Oct	Leaf out to leaf off	Hot-Cool	Temperature and rut	61
Early Winter	1 Nov – 31 Dec	Dormant season; woody/evergreen	Warm-Cold	Potentially metabolism	61
Late Winter	1 Jan – 15 April	Dormant season; woody/evergreen	Cold-Warm	Potentially snow and metabolism	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.

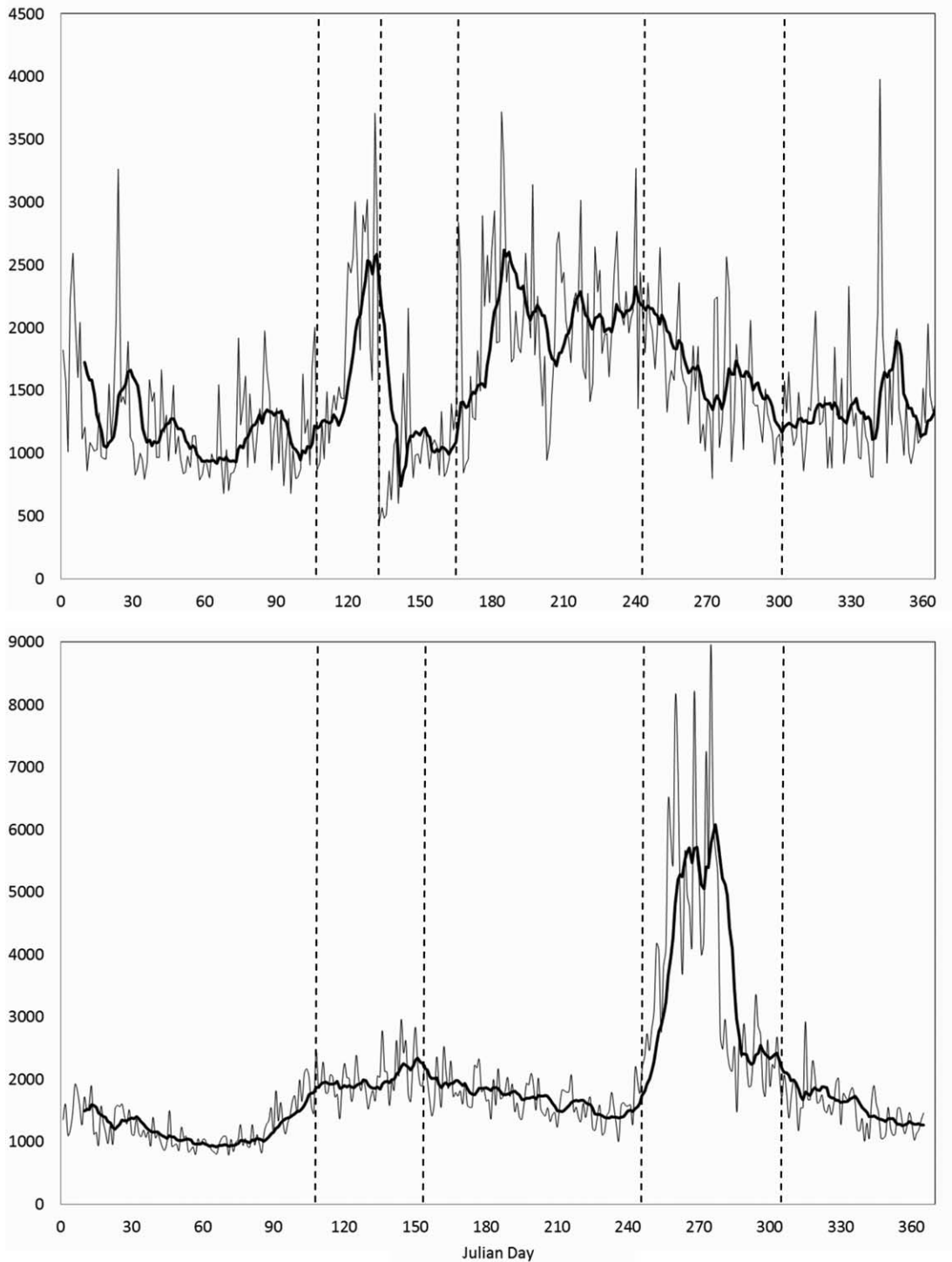


Fig. 1. The Y-axis represents mean daily movement rates (m/day, thin line) for female (top; $n = 5$) and mature male (bottom; $n = 10$) moose in Massachusetts, 2006–2011. The heavy line represents a 10-day moving average to remove noise; the vertical dashed lines mark *a priori* delineated season boundaries.

Choice of the kernel bandwidth or smoothing factor (h) is known to have the greatest effect on the resultant utilization distribution when using kernel density estimators (Worton 1989). A large h over-smooths the data resulting in a positively biased UD that encompasses unused habitats, whereas a small h under-smooths the data resulting in a fragmented UD (Fieberg 2007, Fieberg and Börger 2012). Quantitative methods of determining h can be influenced by sample size, sampling intensity, and the distribution of locations (Kie et al. 2010, Fieberg and Börger 2012), and 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, Fieberg and Borger 2012). We chose a 200-m bandwidth because it strikes a balance between creating a continuous polygon and over-buffering the edges of the utilization distribution. The 200-m bandwidth value merged closely separated locations into a single polygon, but did not merge widely spaced clusters. Mitchell and Powell (2008) noted that fragmentation of UDs may be desired to identify used and unused areas in patchy and fragmented landscapes. Increasing the bandwidth beyond 200 m resulted in UDs with a larger buffer around all points, but failed to further merge disjointed polygons into a single polygon unless very large values of h were used. Smaller values of h resulted in more fragmented UDs that did not accurately represent space use.

Road densities in MCP home ranges and UDs were calculated using the MassEOT (Massachusetts Executive Office of Transportation) roads layer (Massachusetts Office of Geographic Information 2005). We used a 2005 Land Use layer (Massachusetts Office of Geographic Information 2005) to calculate amount of forest and wetlands, and the Protected and Recreational Open Space layer (Massachusetts Office of

Geographic Information 2005) to calculate amount of protected area.

Movements

We calculated mean seasonal daily movement rates by calculating the distance between successive fixes and summing those distances for each 24-h period beginning at 0:00. Mills et al. (2006) showed that decreased GPS sampling intensity resulted in reduced observed movement rates in wolves (*Canis lupus*) due to a reduction in tortuosity of the path. We corrected for the variable sampling rate in our collars (135, 75, and 45 min) by subsampling the more intensively sampled datasets (45 min), and taking every other and then every third location to simulate 90 and 135 min intervals, respectively. We saw a consistent reduction in movement rates with increasing sampling interval. Therefore, we used this information to weight the movements observed in our 135- ($n = 23$) and 45-min ($n = 2$) collars to the intermediate 75-min ($n = 5$) sampling level, making comparisons among individuals possible.

Statistics

We used the R statistical package, version 2.12.2 (R Development Core Team 2005) for all statistical analyses. We used mixed effect models in the R-package lme4 (Bates et al. 2012) to analyze the differences in seasonal home range size and movement rates within and between sexes and seasons. We incorporated random intercept in the models to account for unequal sample sizes among sexes and seasons and to account for repeated measures on individual moose and performed post-hoc pairwise comparisons using the R-package LMERConvenience-Functions (Tremblay and Ransijn 2012). We employed one-sample z-tests to compare road densities in the valley bottoms and uplands to home ranges. Transformations failed to meet the assumption of normality;

therefore, we used a nonparametric paired Wilcoxon's rank-sum test to make comparisons in road density between MCP home ranges and UDs. Significance level for all analyses was set at 0.05.

RESULTS

Capture and Deployment of GPS Collars

We deployed GPS collars on 21 moose: 5 adult (>3 yr) females, 7 adult males, and 1 immature (<3 yr) male in central Massachusetts, and 4 adult and 4 immature males in western Massachusetts; 9 were recaptured to replace GPS collars. We obtained 127,408 locations of the 21 moose with an overall fix rate of 85%. Seasonal data for any animal were only included in the analyses if data were obtained across the entire season. The median number of locations/animal/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 Ranges and Space Use

Mean annual (MCP) home range sizes were not different for mature males (88.8 km²) and females (62.2 km²) ($P = 0.28$; Table 2). Ranges of immature males were larger in all seasons and annually (177.5 km²) than either mature males or females, except for females during summer. There were no differences in mean seasonal range sizes for mature males and females ($P \geq 0.22$), with the exception of fall (23.0

and 59.4 km² for females and males, respectively; $P = 0.002$) (Table 2). Seasonal home ranges for females ranged from 23.0 km² during fall and early winter to 34.8 km² in summer, with no difference ($P \geq 0.32$) in seasonal home range size. Seasonal home range size for mature males ranged from 17.5 km² in late winter to 59.4 km² during fall, with fall home ranges larger ($P \leq 0.01$) than all other seasons.

Mean annual 95% UD sizes were not different between females (26.7 km²) and mature males (28.8 km²) ($P \geq 0.54$; Table 3). Seasonal UD size for females did not differ among seasons ($P \geq 0.07$; Table 3). Seasonal UD size for mature males ranged from 8.5 km² in late winter to 19.6 km² during fall, with fall larger ($P \leq 0.01$) than summer and early and late winter; additionally, spring and summer UDs were larger ($P \leq 0.01$) than late winter. Mature males had larger UDs than central females in fall ($P \leq 0.01$). Seasonal UDs were between 40–51% and 33–63% of seasonal MCP home ranges for females and mature males, respectively.

Location and Composition of Home Ranges and Utilization Distributions

MCP home ranges consisted of 84% (SE = 0.02) forested cover types and 12% wetlands (SE = 0.02), and UDs were 88% (SE = 0.01) forested with 9% (SE = 0.01) wetlands. Conservation land (state forests,

Table 2. Seasonal and annual mean 100% minimum convex polygon home ranges (km²) for females, mature males (estimated >3 yr old), and immature male moose in Massachusetts, 2006–2011.

Season	Central females				Mature males				Immature males			
	n	Mean	SE	Range	n	Mean	SE	Range	n	Mean	SE	Range
Spring	5	26.9	4.2	14.1–39.0	9	28.0	3.2	14–39.0	5	61.4	25.5	15.8–158.1
Summer	5	34.8	7.4	18.2–61.4	8	21.9	4.5	6.2–39.5	4	32.5	6.8	16.2–48.5
Fall	5	23.0	3.7	12.8–28.8	8	59.4	15.1	31.8–161.3	5	222.6	110.0	6.6–546.8
Early Winter	4	23.0	2.9	14.9–29.1	10	29.6	5.4	14.3–72.9	5	50.8	11.9	14.6–83.1
Late Winter	5	25.8	3.8	14.3–38.0	11	17.5	2.7	5.1–31.8	5	33.2	12.8	9.3–80.4
Annual	5	62.2	7.7	41.6–78.4	9	88.8	16.8	49.3–199.4	4	177.5	96.0	33.5–458.9

Table 3. Seasonal and annual mean 95% fixed kernel utilization distribution (km²) for females, mature males (estimated >3 yr old), and immature male moose in Massachusetts, 2006–2011 (smoothing factor (h) = 200 m).

Season	Females				Mature Males				Immature Males			
	n	Mean	SE	Range	n	Mean	SE	Range	n	Mean	SE	Range
Spring	5	10.8	0.8	8.2–12.8	9	15.5	1.4	10.4–22.0	4	19.6	3.7	13.5–28.8
Summer	5	15.9	2.8	8.7–24.4	8	13.9	2.3	5.2–22.5	4	15.4	0.6	13.9–16.4
Fall	4	11.4	0.8	10.0–13.6	7	19.6	2.4	10.4–30.6	4	22.2	8.1	6.5–44.8
Early Winter	5	11.4	1.5	8.4–15.8	9	11.5	0.8	6.3–14.5	4	19.5	1.2	16.5–20.2
Late Winter	5	13.1	0.7	11.6–15.7	10	8.5	1.3	4.1–15.1	4	13.5	4.4	7.4–26.2
Annual	5	26.7	2.0	19.9–32.1	7	28.8	2.4	22.6–41.2	4	37.7	6.8	20.2–51.0

wildlife management areas, other protected land, and conservation easements) made up more of MCP home ranges (60%, SE = 0.05, $P \leq 0.001$) and UD (66%, SE = 0.07, $P \leq 0.001$) than was available as a whole in the Central Uplands (43%), and more in the MCP home ranges (59%, SE = 0.1, $P \leq 0.004$) and UD (76%, SE = 0.1, $P \leq 0.001$) than was available in the Berkshire Hills of western Massachusetts (32%). Additionally, conservation land made up a greater percentage of UD than either the overall MCP home ranges, or the area outside the UD but within the MCPs (the unused portion of the MCP home range) ($P \leq 0.01$); however, there was no difference in the amount of conservation land in MCP home ranges compared to the unused portion of the MCP ($P = 0.16$).

All paved road types were at lower density within home ranges and UD compared to both the valley bottoms and uplands overall ($P \leq 0.001$; Table 4). Additionally, all classes of paved roads (state highways, major local arteries, and local paved roads) were at lower densities within UD than either the overall MCP home ranges, or the unused portion of the MCP home range ($P \leq 0.04$; Fig. 2). State highways and local paved roads were also at greater densities in the unused portion of the MCP than in the overall MCP ($P \leq 0.008$).

Seasonal Movement Patterns

Daily movement rates for female moose in central Massachusetts were consistently ~1,000–1,500 m/day in late winter (Fig. 2).

Table 4. Mean densities (km/km²) (SE) of paved and unpaved roads in the valley bottoms, uplands, within Maximum Convex Polygon (MCP) but outside Utilization Distributions (UD), MCP home ranges, and UD for moose in Massachusetts, 2006–2011.

	Valley Bottoms	Uplands	MCP outside UD	MCP	UD
Interstate Highways	0.08	0.01	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Major State Highways	0.03	0.00	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
State Highways	0.33	0.18	0.13 (0.03)	0.11 (0.03)	0.06 (0.01)
Major Local Arteries	0.31	0.09	0.05 (0.02)	0.03 (0.01)	0.01 (0.01)
Local Paved Roads	1.48	0.50	0.40 (0.05)	0.30 (0.08)	0.14 (0.09)
Local Unpaved/Improved Forest Roads	0.39	0.48	0.54 (0.06)	0.49 (0.13)	0.44 (0.03)
Forest Roads	0.73	0.28	0.33 (0.04)	0.35 (0.09)	0.38 (0.07)

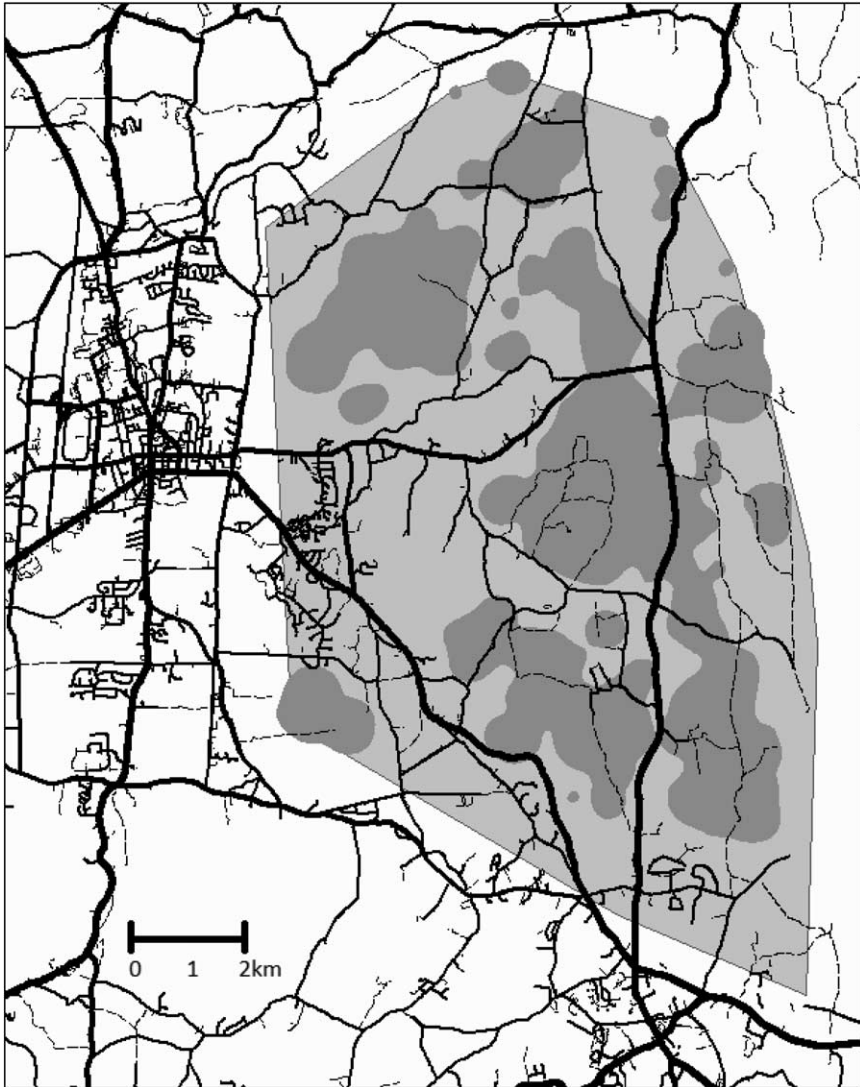


Fig. 2. Road density in annual fixed kernel utilization distribution (dark gray) and minimum convex polygon home range (light gray) for a representative moose in Massachusetts. Heavy lines are major local roads and state highways, thin solid lines are local paved roads, and dashed lines are forest roads with limited access.

In spring, daily movement nearly doubled to $\sim 3,000$ m/day prior to calving. There was a sharp decline to 500 m/day the second week of May that corresponded with the observed 8–13 May calving period. Mean daily movement rates remained low for May and most of June, before peaking at $\sim 3,000$ m/day in early July and remaining high for the remainder of the summer. Movement rate declined in

September to about 1,500 m/day and remained fairly consistent for the rest of the year. Spring and summer seasonal movement rates for females were greater than all other seasons and calving season movement rates were lower than all other seasons ($P \leq 0.05$; Table 5).

Daily movement rates were lowest (1,000 m/day) for mature males from the

Table 5. Seasonal daily movement rates (m/day) for female and mature male moose in Massachusetts. Mean seasonal daily movement rates and (SE) in light gray, *P*-values for seasonal comparison between males and females in dark gray, *P*-values for comparisons among seasons for females above the diagonal and for males below the diagonal.

				Female					
				Spring	Summer	Fall	Early Winter	Late Winter	Calving
		Mean		2391 (141.0)	2464 (216.6)	1837 (81.5)	1505 (158.0)	1492 (107.9)	874 (70.6)
				SP	0.719	0.012	<0.001	<0.001	<0.001
Mature Male	Spring	2019 (161.3)	SP	0.22	SM	0.006	<0.001	<0.001	<0.001
	Summer	1731 (120.5)	0.168	SM	0.017	FL	0.112	0.097	<0.001
	Fall	3542 (385.2)	<0.001	<0.001	FL	<0.001	EW	0.951	0.008
	Early winter	1514 (107.0)	0.017	0.291	<0.001	EW	0.967	LW	0.009
	Late winter	1103 (79.8)	<0.001	0.004	<0.001	0.051	LW	0.157	

beginning of February until the end of March (Table 5). Movements increased in early April and peaked at ~2,500 m/day in late May and early June, before declining as summer progressed. Daily movements increased to 3,000 m/day during the second week of September, indicating the start of the rut. Movements increased further to a peak of nearly 8,000 m/day the last week of September and remained high through the first week of October, then declined sharply. Movement rates remained relatively high at 2,000–2,500 m/day until the beginning of December when they declined to winter levels of 1,000–1,500 m/day. Fall seasonal movement rates were greater than in all other seasons for mature males (*P* ≤ 0.05; Table 5); additionally, spring and summer rates were greater than in late winter, and spring was greater than early winter. Male daily movement rates were greater (*P* ≤ 0.05) than females during fall and lower during summer.

DISCUSSION

Home Range as a Measure of Resource Use

Spatial requirements as measured by home range (second order use; Johnson 1980) and UDs (i.e., measuring use patterns

within the home range; third order use) can provide important information about productivity of available habitat, distribution of resources and limiting factors, and how a species uses resources. This information is critical for conservation planning and habitat protection and connectivity at local and regional scales, and is particularly relevant for large mobile mammals in highly developed landscapes with fragmented patches of protected lands.

Harris et al. (1990) recommended using at least 2 home range estimators for all animal location data sets, including minimum convex polygon (Mohr 1947) because of its prevalent use and comparability among studies. A MCP home range measures the area used by an individual to fulfill its annual or seasonal needs, but it does not describe how the area is used. Alternatively, UDs created by fixed kernels (Worton 1989) describe the pattern and intensity of use within the MCP home range. By examining both, we can quantify areas of actual and relative intensity of use, identify important seasonal habitat patches, and delineate the area of landscape required to provide those patches

Comparison of UDs to MCPs shows that moose in southern New England used the

landscape in a patchy manner; UDs were typically only half the size of MCPs, meaning that at any time there was a 95% probability of locating a moose within <50% of the MCP home range. Additionally, UDs fragmented into multiple polygons, indicating that resources were patchily distributed. Maintaining connectivity of used patches within the larger landscape (MCP and larger) is essential for moose and other wide ranging species.

Rettie and Messier (2000) argued that selection at the scale of the home range reflects attempts to reduce the effects of limiting factors. The UDs measured here were located almost exclusively on the uplands of the central and western parts of the state, with limited use of valley bottoms. When valley bottoms were included in an MCP home range, they were mostly unused portions that were traversed in movements between ridge tops. Overall, UDs had greater amounts of forested habitat and conservation land and lower road densities than the landscape as a whole, or than the MCP home ranges. By definition moose spent 95% of their time in these less developed areas and appeared to select for more heavily forested areas away from human development. Moose often crossed roads of all types in Massachusetts, but seemed to show less avoidance of local residential roads with lower traffic volumes and speed limits than major highways, state highways, and major local arteries. In many instances major roads formed boundaries at the edge of an individual's home range; in other cases home ranges were bisected by highways and main roads. Use of higher elevations could also be an attempt to limit thermal stress by taking advantage of reduced ambient temperatures and increased exposure to convective cooling from wind. Human development and associated vehicle traffic and high temperatures that result in thermal stress

may be limiting factors for moose in Massachusetts.

Seasonal Home Ranges

In central Massachusetts, female MCP home ranges were largest during summer when energy demands were greatest because of lactation and seasonal restoration of body condition. Mature male home ranges were largest during fall when they search for and attend mates during the breeding season, and smallest during late winter and summer when movements were presumably restricted by the combined effects of lower metabolism, snow conditions, and thermoregulatory constraints.

Despite the large number of studies on home range size (Hundertmark 1997), comparisons to our results must be made with caution. Most studies have used traditional VHF telemetry and home ranges were calculated with a small number of locations (e.g., <30), particularly in winter (e.g., <10), which can underestimate home range size (Kernohan et al. 2001, Börger et al. 2006); further, few VHF locations are collected at night when moose are often active. Kernohan et al. (2001) suggested a minimum number of 30 locations, but at least 50 to calculate an accurate home range. Additionally, differences in methods and the length, timing, and number of seasons used can make comparisons difficult (Kernohan et al. 2001, Börger et al. 2006). Even with these limitations, our results fall within the range presented by Hundertmark (1997) for home range sizes across North America (Fig. 3). Overall, home range size decreased with decreasing latitude and summer and winter home ranges in Massachusetts would be expected at the low end of the scale.

In the northeastern United States our results are similar to those of Leptich and Gilbert's (1989) in Maine with >50 locations for 11 of 13 collared moose and an estimated

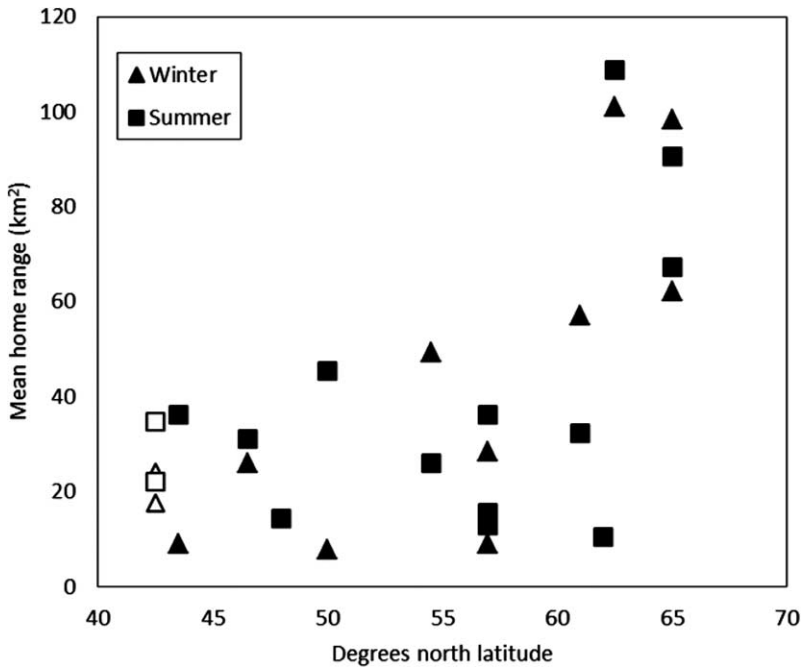


Fig. 3. Mean size of winter and summer home ranges in square kilometers for moose in North America relative to latitude (as reported by Hundertmark 1997). Data for female and male moose added as open symbols.

summer MCP home range of 25 km² for females. Thompson et al. (1995) reported median summer home ranges of 32 km² for females and 28 km² for males in Maine; their sample sizes in other seasons were too low for comparison. Winter ranges were typified by concentrated use of small areas with short movements to other areas of intensive use in Minnesota (Van Ballenberghe and Peek 1971) and Maine (Thompson et al. 1995), a pattern similar to our observations. In northern New Hampshire, Scarpitti et al. (2005) observed smaller seasonal home ranges for females than our study (≤ 17 km² for all seasons), with an earlier study in northern New Hampshire (Miller and Litvaitis 1992) reporting much larger annual home ranges for females (153 km²) with the largest seasonal home ranges during fall (82 km²). Garner and Porter (1990) reported 36 km² for summer and 8 km² for winter home ranges of

males in the Adirondack Mountains of New York. Our seasonal results are the opposite of Lenarz et al. (2011) who reported smaller home ranges during summer (16 km²) than in winter (33 km²) in Minnesota.

Movements

Seasonal activity and movement patterns reflect changes in metabolic rate, ruminating time, and activity associated with the annual cycle of vegetation growth in temperate forests (Risenhoover 1986, Cederlund 1989). Increased movement rates in spring corresponded with the start of the growing season and increased abundance and quality of browse. High movement rates in summer have been shown to reflect increased activity associated with more foraging bouts, lower ruminating times, and an attempt by moose to maximize foraging during the growing season (Belovsky 1981, Cederlund 1989,

Van Ballenberghe and Miquelle 1990). We speculate that the periodically reduced rates in movements we observed during spring, summer, and fall were the result of thermoregulatory behavior during periods of high temperatures.

The reduced movements during winter were typical of moose throughout their range (Phillips et al. 1973, Dussault et al. 2005, Schwartz and Renecker 2007). Schwartz and Renecker (2007) suggest that the lower winter metabolic rate of moose is an adaptation to counteract reduced forage abundance and quality and the related increased time required to digest a highly fibrous diet, resulting in fewer feeding bouts and lower activity level. Movements were further reduced during periods of deep snow; however, snow depth and condition vary annually and across the state with the highest likelihood of deep snow at higher elevations in western Massachusetts. When confined by deep snow, moose concentrated their habitat use into as little as 0.5 km² for up to 3.5 months. The variability in the timing, depth, and condition of snowfall strongly influenced the variability of home range size and movements in early and late winter, as moose moved widely between suitable winter habitats until confined by snow. In addition to the influence of seasonal patterns on movements, changes in daily movement rates were greatest at times of the year corresponding to the annual reproductive cycle, i.e., calving for females and the rut for males.

A final important consideration for understanding movements of moose in southern New England is the lack of their major predator, wolves (*Canis lupus*), and the absence of moose hunting. Predators and hunters can play important roles in the distribution and movements of their ungulate prey. Black bears (*Ursus americanus*) and coyotes (*Canis latrans*) may prey on some moose calves, but in general the influence

of predators or hunters on moose movements and distribution is absent in Massachusetts.

MANAGEMENT IMPLICATIONS

Existing distribution of vegetative communities, landscape configurations, and levels of development have allowed moose to re-colonize and establish a low density population throughout central and western Massachusetts and into Connecticut after 200–300 years of absence. However, southern New England is comprised of some of the most densely populated and highly developed states in the nation, and despite very active and successful conservation agencies and organizations, the trend will continue to move in the direction of more development and increased fragmentation. We have documented key elements of habitat use and movement distances and patterns by this newly re-established moose population. This information can be used to further enhance existing high priority conservation areas and identify new areas for protection and landscape connectivity. Massachusetts has many well established biodiversity conservation initiatives (e.g., Wildlife BioMap and Living Waters) and planning strategies should recognize and incorporate a suitable scale to accommodate moose. If this large-scale challenge can be met, biodiversity conservation will benefit because moose use a diversity of terrestrial and wetland vegetative types (composition, size, and structure) that provide habitat for a wide array of species.

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