



Status, Movements, and Habitat Use of Moose in Massachusetts

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**STATUS, MOVEMENTS, AND HABITAT USE OF MOOSE IN
MASSACHUSETTS**

A Thesis Presented

by

DAVID WILLIAM WATTLES

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

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Department of Environmental Conservation
Wildlife & Fisheries Conservation

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ABSTRACT

STATUS, MOVEMENTS, AND HABITAT USE OF MOOSE IN MASSACHUSETTS

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Moose (*Alces alces*) have been re-established in much of the historic range in the northeastern United States. Recently the southern edge of the species ranges has been extended southward into southern New England and northern New York from established populations in northern New England. The southern expansion raised questions as to the ability of this northern species to cope with higher temperatures, areas densely populated by humans, and different forest types further south. In light of these recent developments, we conducted a literature search on moose in the northeastern United States and distributed a questionnaire and conducted phone interviews with biologists responsible for moose management across the region to determine the status and management of moose in New England and New York. Furthermore, in 2006 we initiated a study on the home ranges, movements, and habitat use of moose in Massachusetts. We captured and collared moose with Global Positioning System (GPS) collars to track their movements in the Commonwealth. The surveys and interviews with the state biologists revealed that moose populations appeared to be stabilizing in southern New England. However, the moose population continued to grow in northern New York. Moose populations in northern New England were managed with an annual fall harvest, but moose hunting was

not allowed in southern New England or New York. Throughout the region moose vehicle collisions were a major concern (>1,000 occur each year) including several that resulted in human fatalities. The collaring study has revealed the importance of maintaining a variety of forest cover types, age classes, and wetland habitats to meet the seasonal needs of moose, including early successional habitats created by logging that appear to be important for moose. Mean home range sizes were 64.9 km^2 ($SE = 12.9$) and 73.3 km^2 ($SE = 9.4$), respectively, for females and males in central Massachusetts, and 164.5 km^2 ($SE = 62.6$) for males in western Massachusetts. Moose often interacted with roads and human development on the uplands, but used less developed areas of their home ranges. This demonstrates the importance of preserving the integrity and connectivity of the forested landscape of Massachusetts.

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CHAPTER 1

STATUS AND MANAGEMENT OF MOOSE IN THE NORTHEASTERN UNITED STATES

1.1 Introduction

Although exact records of historic moose (*Alces alces*) distribution and numbers are difficult to come by, Goodwin (1936) claimed through anecdotal evidence that moose once ranged as far south as the Alleghany Mountains of Pennsylvania in eastern North America. By 1870, however, moose had likely been eliminated throughout the southern portion of the range through unregulated and commercial hunting and clearing of forests for agriculture. Allen (1870) claimed that moose were extinct in Massachusetts, southern Vermont, southern New Hampshire, and southern Maine, but at this time could still be found in northern portions of Maine, and likely in northern New Hampshire, Vermont, and the Adirondack Mountains of New York.

The eventual recovery and expansion of moose populations in the northeast likely resulted from a number of factors, the 2 most important being regulation of moose hunting and reforestation of abandoned farmland. Maine was the last state in the region to protect moose from hunting. The 1936 closure of the hunting season in Maine protected moose throughout the northeastern United States, and as farms were abandoned across the region, reforestation – and subsequent logging that created patches of younger forest amid even-aged stands – increased and improved available habitat for moose (Alexander 1993, Bontaites and Guftason 1993). Other factors that likely influenced moose population increases were the spread and reintroductions of beavers (*Castor canadensis*) and the corresponding increase in wetland habitat, and the decline of white-tailed deer

(*Odocoileus virginianus*) populations and resultant decrease in the parasite *Parelaphostrongylus tenuis* (Alexander 1993, Bontaites and Guftason 1993).

By the 1970s moose had increased to sufficient numbers in Maine to expand into adjacent New Hampshire, augmenting the small population there, so that by 1977 there were about 500 moose in New Hampshire (Bontaites and Guftason 1993). Exploiting unoccupied habitat, moose in New Hampshire quickly increased to about 1,600 in 1982 and 5,000 by 1993 (Bontaites and Guftason 1993). The same pattern was followed in Vermont, with the moose population increasing from 200 in 1980 to 1,500 in 1993, when the population was first hunted again (Alexander 1993).

Despite the historical presence of moose in southern New England, many moose biologists considered the region to have marginal habitat and thought it unlikely that moose would establish viable populations in those habitats (Karns 1997; W. Woytek, Massachusetts Division of Fisheries and Wildlife, personal communication). Chief among the challenges for moose is the human-dominated landscape and the high potential for conflict with people (Vecellio et al. 1993, Peek and Morris 1998). Other factors that could impede the successful reestablishment of moose populations in southern New England include the highly fragmented mid-late stage mixed deciduous forest, relatively limited early successional habitat, and lack of key browse species found in the boreal forest, such as balsam fir (*Abies balsamea*), willow (*Salix* spp.), mountain ash (*Sorbus aucuparia*), and trembling aspen (*Populus tremuloides*). The forests of New England transition from northern forest types dominated by spruce (*Picea* spp.), balsam fir, American beech (*Fagus grandifolia*), birch (*Betula* spp.), Eastern hemlock (*Tsuga canadensis*), and maple (*Acer* spp.), where moose are common, to transitional hardwood

forests increasingly dominated by oak (*Quercus* spp.) and white pine (*Pinus strobus*), where little is known about moose habitat requirements. Northern New York state and the forests of the Berkshire Mountains in western Massachusetts are more similar to forest communities of northern New England. Additionally, the higher temperatures in southern New England increase the likelihood of negative impacts due to thermal stress (Renecker and Hudson 1986, Murray et al. 2006, Lenarz et al. 2009). Moose must also cope with high deer densities and the effects of the associated parasite *P. tenuis*; however, the effects of this parasite are not thought to be as severe as was once believed (Whitlaw and Lankester 1994).

These factors did not stop moose from expanding out of Vermont and New Hampshire and into Massachusetts in the 1960s. Before 1966, Massachusetts had few public reports of moose; however, almost every year thereafter at least one moose sighting was reported. Based on this, Vecellio et al. (1993) determined that moose began re-colonizing Massachusetts in 1966. Hicks (1986) stated that regular occupation of New York by moose began in 1980, initially in the border regions near Quebec, Ontario, and Vermont, but spread quickly throughout the Adirondack Mountains in the northern third of the state. By the late 1980s and early 1990s moose began showing up in Connecticut, and by 1998 there was evidence of a breeding population (Kilpatrick et al. 2003). Moose are now well established in New York, Massachusetts, and Connecticut.

To understand moose status and management, the northeastern United States can be divided into two regions based on the timing of when moose became established and the size of the populations. Northern New England includes Maine, New Hampshire, and Vermont, where moose populations are well established and have been actively managed

for several decades. Southern New England and New York includes Massachusetts and Connecticut (currently there are no resident moose in Rhode Island) and upstate New York, where moose are more recently established and management policies are still being formed. There are management issues that are distinct between the regions, as well as issues that are common to both regions, such as moose-vehicle collisions. Our objectives are to report on the current status of moose populations and management policies in the northeastern United States, to discuss differences and similarities between northern and southern New England and New York, and to recommend further research and management strategies to better understand and manage moose populations in the region.

1.2 Study Area

The northeastern states of Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and New York currently have resident moose populations. In addition, Rhode Island, New Jersey, and Pennsylvania are northeastern states where moose were found historically (Goodwin 1936; L. Gibson, Rhode Island Division of Fish & Wildlife, personal communication; C. Condolf, New Jersey Division of Fish and Wildlife, personal communication). New York and the New England states of Connecticut and Massachusetts represent the southern edge of moose range in eastern North America. In western North America moose reach as far south as Colorado and Utah in the Rocky Mountain region. Moose populations in the northeastern U. S. fall between 66° 57' W longitude in eastern Maine and 76° 10' W longitude on the western side of the Adirondack Mountains in New York, and between 47° 28' N latitude in northern Maine and 41° 38' N in central Connecticut (Ed Reed, New York Department of Conservation, Bureau of Wildlife, personal communication; H. Kilpatrick, Connecticut Department of

Environmental Protection, personal communication; L. Kantar, Maine Department of Inland Fisheries and Wildlife, personal communication) (Fig. 1.1).

New Jersey, Rhode Island, Massachusetts, and Connecticut are the most densely populated states in the nation (U.S. Census Bureau n.d.). As a result, human development and road networks dominate these states, making forest habitat patchy and highly fragmented. Southeastern New Hampshire and coastal southeastern Maine also have high levels of human development. In general, human densities decrease to the north and west in the region as forested area and available moose habitat increases.

The northeastern United States is heavily forested, with extensive streams, rivers, lakes, ponds, and wetlands. Elevations range from sea-level to 1,916 m in the White Mountains of New Hampshire. DeGraaf and Yamasaki (2001) identified 5 main forest regions in New England and New York, which make up the forests of moose range. Each has characteristic tree species and is associated with specific physiographic and climatic conditions. Spruce-Balsam Fir forests occur in the coldest area of the northeast, above 150 m in Maine, and at higher elevations in New Hampshire, Vermont, and New York. Northern Hardwoods-Spruce Forests are associated at lower elevations in Maine and are found below 850 m in mountains of New Hampshire, Vermont, and northern New York. Small pockets of this forest type can be found in the mountains of western Massachusetts. Northern Hardwood forests are found between 150 and 790 m in Maine, and in New Hampshire, Vermont, New York, and western Massachusetts. Transitional Hardwoods-White Pine forest is found at lower elevations in the uplands of northern New England and is the dominant forest region in Massachusetts and northeast Connecticut. The Central Hardwoods-Eastern Hemlock-White Pine forest region is found throughout

Connecticut, southern and eastern Massachusetts, and extreme southeastern New Hampshire and Maine (DeGraaf and Yamasaki 2001).

1.3 Methods

We conducted a survey by electronic mail (email) of state fish and wildlife agency deer and moose biologists for the northeastern states that have established moose populations: Maine, New Hampshire, Vermont, Massachusetts, New York, and Connecticut. We asked about the abundance, distribution, and status of the moose population, population goals for moose in the state, state management practices including hunting and habitat management, issues or concerns regarding moose, and experience with public perceptions. We asked follow-up questions via telephone and email when additional information or clarification was needed. We also conducted telephone interviews with the deer biologists for Rhode Island, New Jersey, and Pennsylvania (all states adjacent to states with moose populations and where moose were reportedly found historically) and asked them about moose sightings or any anecdotal information on moose in their state. We also gathered, reviewed, and summarized literature on the status and management of moose populations in the northeastern U. S.

1.4 Results

1.4.1 Southern New England and New York

1.4.1.1 Massachusetts

Moose numbers increased rapidly in Massachusetts in the 1990s after originally re-colonizing the state in the 1960s. The Massachusetts Division of Fisheries and Wildlife (MDFW) estimated the state moose population to be about 850-950 in 2010. A regression model, originally developed in New Hampshire (Bontaites et al. 2000; S. Christensen, Massachusetts Division of Fisheries and Wildlife, personal communication), uses both moose sightings reported in deer hunter surveys and available suitable habitat to arrive at estimates of moose abundance. Based on this method, the population appeared to have stabilized in Massachusetts since 2001, with the possible exception of the Berkshires Hills region in the western portion of the state, where it may still be increasing slightly. The Massachusetts Division of Fisheries and Wildlife would like to maintain the population at the 2010 level, with the overall goal “to maintain and sustain a resident breeding moose population in the state in areas of suitable habitat throughout its historic range at levels which support ecological and cultural values while minimizing human-moose conflicts” (S. Christensen, Massachusetts Division of Fisheries and Wildlife, personal communication).

Moose habitat in Massachusetts is found primarily in the central and western portions of the state, west of the city of Worcester, though moose have been frequently reported east of Worcester. This area constitutes the greater Boston metropolitan region, and patches of suitable habitat become smaller and more fragmented. High human population densities make it likely that moose in this area will be considered problem

animals. In western Massachusetts the 2 main forest regions are separated by the Connecticut River Valley and the Interstate 91 highway corridor, both of which run N-S. These regions are fragmented by state highways and towns, but enough forest habitat remains to support a stable moose population.

As the number of moose in Massachusetts began to increase in the late 1980s and early 1990s, Vecellio et al. (1993) and McDonald (2003) raised questions as to the ability of a state as densely populated as Massachusetts to coexist with a growing moose population. Massachusetts has the third highest density of people in the country, averaging about 313 people per km² (U.S. Census Bureau n.d.). They speculated that the cultural carrying capacity would be exceeded and the situation would become untenable and, unless proactive management was used, conflict would be inevitable. As predicted, the moose population in Massachusetts began to increase rapidly after 1993. The number of moose-vehicle collisions (MVC) increased as well, increasing steadily from the early 1990s (Vecellio et al. 1993; Massachusetts Division of Fisheries and Wildlife, unpublished data) to a peak of 52 reported MVCs in 2004 (Fig. 1.2). Two human fatalities resulting from automobile accidents with moose have occurred in the state, in 2003 and 2007 (Table 1.1).

Despite the increase in costly and dangerous MVCs, moose have not apparently exceeded cultural carrying capacity and public perception of moose in Massachusetts seems to be almost universally positive, based on MDFW's and our interactions with the public. Moose densities in Massachusetts are low relative to most of the moose geographic range and this, combined with dense deciduous forest cover, makes moose sightings still something of a novelty. In fact, it is likely the vast majority of people in

Massachusetts have never seen a moose in the state. The MDFW regard the return of moose to Massachusetts as a conservation success story.

As of 2010, MDFW does not have the authority to actively manage the moose population with a harvest because moose hunting is specifically prohibited by statute. Legislation was first introduced in 2002 to give MDFW the ability to manage moose, but the bill has not progressed beyond the legislative committee stage. There is interest from hunters to initiate a moose hunt in Massachusetts, but there is also a large animal rights and anti-hunting population in Massachusetts.

Existing management activities include monitoring moose vehicle collisions and continued analysis of deer- hunter moose sightings. The most direct form of management is in response to problem animal situations. Massachusetts has developed a Large Animal Response Team (LART) composed of MDFW and Environmental Police personnel, which responds to problem animal situations involving moose and other large mammals. Problem animal situations occur when a moose becomes a threat to public safety or their own safety by wandering into towns or onto busy roadways. The current policy has 3 stages: (1) if possible, the animal is hazed or herded out of the developed area and back into suitable habitat; (2) if hazing fails and immediate public safety is not an issue, the animal is immobilized and relocated to a wildlife management area, state forest, or other suitable area away from development; and (3) finally, if the animal is an immediate threat and hazing and immobilization are not feasible, it can be euthanized. Over the past 10 years, the Massachusetts LART has performed between 1 and 9 relocations and 0 and 5 public safety kills annually in response to problem moose situations. The number of

problem animal responses of all types, including those that resulted in relocating or euthanizing a moose, has declined over the last 5 years.

Another growing concern about moose in Massachusetts comes from wildlife ecologists, foresters, and private land managers. In the forests of southern New England, as elsewhere, regenerating forests are an extremely important source of browse for moose, with moose using early successional habitat created by logging 50-65% of the time, depending on season (Massachusetts Cooperative Fish and Wildlife Research Unit, unpublished data). As the moose population has grown, impacts from moose browsing on regenerating forest have increased. Large tracts of managed state land tend to be able to support higher moose densities and appear to have seen greater browsing impacts. Foresters and larger commercial logging companies in the state are growing increasingly concerned with the long term impacts of moose browse on the species composition and structure of Massachusetts forests.

Researchers in Massachusetts are attempting to learn how moose use the landscape, respond to the dense human populations, cope with high temperatures, and interact with the deciduous forest and forest regeneration. Beginning in 2006, the USGS Massachusetts Cooperative Fish and Wildlife Research Unit, in conjunction with MDFW, began to study movements and habitat use of moose equipped with global positioning system (GPS) collars ($n = 35$). Faison et al. (2010) recently completed a study on moose browsing in the deciduous forest of Massachusetts, and there are plans to incorporate vegetation studies with the GPS data to further evaluate moose diet in this environment. In addition, several sets of 20 x 20 m fenced exclosures have been built in southern New England, with paired control plots, to estimate the effects of moose browsing on species

composition and rate of forest regeneration (Compton and DeStefano 2009, Faison et al. 2010).

1.4.1.2 New York

Moose began re-colonizing New York State around 1980, with animals dispersing from Vermont and Canada. By 1990, the population was estimated at about 20 animals, with a 3:1 bull to cow ratio, typical of a colonizing population (Garner and Porter 1990). In the early 1990s the New York Department of Environmental Conservation, Bureau of Wildlife (DEC) considered augmenting the growing population with relocated moose, but decided against this due to lack of public support because of concerns over increased moose-human conflict and a desire for moose to repopulate naturally (Hicks and McGowan 1992, Lauber and Knuth 1997).

The moose population in New York has grown steadily since the early 1990s as moose exploited unoccupied habitat. The DEC estimated the 2008 moose population to be between 300-500 animals, with most in and around the 25,000-km² Adirondack Park and Reserve in the northern third of the state (Fig. 1.1). Moose were also present and appeared to be increasing in the Taconic highlands on the Vermont and Massachusetts borders, where public observations are increasing. Moose densities were greatest on private land along the northern edge of the Adirondack Park, where forest management was more active. In the Adirondack Reserve, which makes up the majority of moose habitat in the state, logging is not permitted, which may keep moose densities and population growth rates lower than what has been seen previously in Vermont and New Hampshire, where no such restrictions exist. There were very few sightings or reports of moose south of the Interstate 90 corridor, although sightings have become more common

and are usually young bulls, indicating dispersing animals. However, the DEC does not expect moose to become established in southern New York because of the higher levels of development and higher temperatures. State biologists expected the population to exceed 1,000 animals by 2010; however, the growth of the population was slower than predicted and the 2010 population was estimated at 500-800 animals (C. Dente and E. Reed, New York Department of Conservation, Bureau of Wildlife, personal communication).

The New York Department of Conservation's goal is for an increase in moose numbers in northern New York. New York has monitored the growing population through reports of mortalities, reproduction, and public moose sightings. Aerial surveys have been conducted to help determine the distribution of moose in the state, but not to estimate the population. Another source of information to monitor growth of the state's moose population was through a survey of successful deer hunters, conducted by the Wildlife Conservation Society, which asked for reports of moose sightings and moose sign. Response to these surveys was low (10%). Since 2008, DEC has conducted their own surveys and the response rate has increased to 30%. As in other places where moose and deer range overlap, there is concern over the effect of *P. tenuis* in moose, and several cases of brainworm have been documented (C. Dente and E. Reed, New York Department of Conservation, Bureau of Wildlife, personal communication).

Concerns over more moose vehicle collisions with the increasing moose population are growing (Fig. 1.2). The DEC and the state Department of Transportation (DOT) have increased signage and taken other measures to warn the public of the dangers of MVCs, and DOT is investigating moose road crossings and MVCs in the state. Moose

vehicle collisions in more densely populated southern New York, north of New York City, raised concerns in the popular press regarding the need for a moose hunt in New York; however, it is likely these moose were dispersing from Connecticut and Massachusetts and not northern New York (C. Dente, New York Department of Conservation, Bureau of Wildlife, personal communication).

Instances where moose come into conflict with people are increasing. The state has developed a plan to coordinate and standardize response actions across regions, including relocations of moose that become a threat to public safety. Most response actions result from moose wandering into more developed areas in the greater Albany region and Interstate 90 corridor. Moose are currently protected by law in New York, which limits the ability of DEC to manage moose. The Department is looking into the possibility of getting the law changed to allow for potential management actions (such as a limited hunting season) should they be warranted in the future. Despite these concerns, public opinion on moose in New York is very positive and people are excited to have them back in the state (E. Reed, New York Department of Conservation, Bureau of Wildlife, personal communication).

1.4.1.3 Connecticut

According to Kilpatrick et al. (2003), moose began to re-colonize Connecticut in the late 1980s and 1990s, with young bulls dispersing from Massachusetts. By 1990 sightings of females became more common, and by 1998 evidence of a resident breeding population was found, including the first confirmed cow and calf sighting in 2000. Consistent cow-calf sightings were reported since then. The increase in cow-calf sightings corresponded with increasing public moose sightings in general in the late

1990s, from ≤ 5 in the early 1990s up to 32 sightings in 2002 (Kilpatrick et al. 2003). Similarly, there had been no MVCs in Connecticut before 1995, when 2 MVCs occurred. Subsequently, the frequency of MVCs increased, with 1-4 MVCs occurring annually since 2003 (Fig. 1.2) (Kilpatrick et al. 2003; H. Kilpatrick, Connecticut Department of Environmental Protection, personal communication). The first human fatality resulting from a MVC occurred in the state in 2007 (Table 1.1) (A. Labonte, Connecticut Department of Environmental Protection, personal communication).

Most of the moose in Connecticut are located in the more rural and forested northern third of the state, with higher densities in the northwest than northeast (H. Kilpatrick, Connecticut Department of Environmental Protection, personal communication). The 2 areas of moose habitat in Connecticut are largely separated from each other by the heavily developed portion of the Connecticut River Valley between Springfield, Massachusetts and Hartford, Connecticut. However, the northwest and northeast regions are connected to moose habitat in western and central Massachusetts.

In 2008 the moose population in Connecticut was conservatively estimated to be >100 animals and increasing (H. Kilpatrick, Connecticut Department of Environmental Protection, personal communication). Continued growth was expected despite the opinion that high temperatures, range overlap with white-tailed deer and occurrence of brain worm, and marginal habitat should all limit population growth. A subsequent population estimate using a more conservative method in 2010 resulted in a lower population estimate of about 75 animals (A. Labonte, Connecticut Department of Environmental Protection, personal communication). These estimates were based on observation rates and public reports; the latter may be decreasing now that moose are not

the novelty they once were. However, the general trend of stabilization after a slight reduction in population matches what appears to have occurred in Massachusetts and southwest New Hampshire (S. Christensen, Massachusetts Division of Fisheries and Wildlife, personal communication; K. Rines, New Hampshire Fish and Game Department, personal communication).

Connecticut is the fourth most densely populated state in the nation, with 271 people per km² (U.S. Census Bureau n.d.). The high human population, dense road network, and high traffic volumes make coexistence between humans and a large moose population potentially dangerous. Several moose that entered into highly developed or high traffic areas were relocated or euthanized annually by Connecticut Department of Environmental Protection (CDEP) personal. As a result CDEP has concerns about continued growth of the moose population. This concern is based on public safety issues and a desire to keep MVCs at low levels. As a result, Connecticut is conducting public and hunter opinion surveys, preparing a moose management plan, and considering the possibility of initiating a moose hunt to limit population growth. Any initiation of a hunt will likely be met by opposition from anti-hunting groups in the state. The Connecticut Department of Environmental Protection has also initiated a study that employs GPS collars to investigate moose habitat use and movement in the state (H. Kilpatrick, Connecticut Department of Environmental Protection, personal communication).

1.4.2 Northern New England

Maine, New Hampshire, and Vermont have long established moose populations. Moose are an important social, ecological, and economic species in the region. Moose bring in millions of dollars a year to these states both through hunting permits and related

expenditures and wildlife viewing and tourism revenues. The moose populations in Maine, New Hampshire, and Vermont have been actively managed with legal hunting seasons since 1980, 1988, and 1993, respectively. Detailed summaries of the history of moose recovery and initiation and expansion of hunting seasons in these states can be found in Alexander (1993), Bontaites and Guftason (1993), and Morris (2007), as well as annual state hunt summaries. Throughout the region, public participation involving varied stakeholder groups plays a large role in determining management goals (C. Alexander, Vermont Fish and Wildlife Department, personal communication; L. Kantar, Maine Department of Inland Fisheries and Wildlife, personal communication; K. Rines, New Hampshire Fish and Game Department, personal communication). Managers in these states face some similar concerns to the states of southern New England, particularly dealing with MVCs, but must also strike a balance within their own states to meet the sometimes conflicting goals of different interest groups.

1.4.2.1 Maine

In 2010 there were about 30,000 to 60,000 moose throughout the state of Maine. Moose densities vary with higher densities in the forested interior and lower densities along the coast. In the forested interior, densities range from 0.2-0.6 moose per km² in the south to 1.0-1.7 moose per km² in the north (Morris 2007; L. Kantar, Maine Department of Inland Fisheries and Wildlife, personal communication).

In 2000, the Maine Department of Inland Fish and Wildlife (MDIFW) was given full control over moose management regulations by the state legislature (L. Kantar, Maine Department of Inland Fisheries and Wildlife, personal communication). At that time moose management goals and objectives were revised by a public working group.

The working group created a more comprehensive set of goals compared to the previously established goal of keeping the population at 1985 levels (Morris 2007). Goals and objectives continue to be developed through a public participation process involving representative stakeholders, including potentially conflicting groups associated with growing moose watching activities and with moose hunting, both of which are important economically to Maine (Morris 2007). The goal is to strike a balance between moose viewing, public safety, and recreational opportunities (L. Kantar, Maine Department of Inland Fisheries and Wildlife, personal communication). The 2000 guidelines set population objectives specific to each of the 29 Wildlife Management Districts (WMD) and fall into 3 main categories: (1) recreation management, which seeks to maintain the population at 60% of carrying capacity to maximize hunting and viewing opportunities, (2) road safety, which seeks to reduce the population to decrease MVCs, and (3) compromise, which seeks to reduce the population by a third to both decrease MVCs and maintain quality recreational opportunities (Morris 2007; L.Kantar, Maine Department of Inland Fisheries and Wildlife, personal communication).

Wildlife Management Districts in the remote and heavily managed forests of northwestern and central western portions of Maine, where the human population is small, fall into the recreation management category, WMDs along the northeast-eastern and southwest borders of the state are in the compromise category, and WMDs along the more densely populated southern interior and southeastern coastline of Maine are in the road safety category (L. Kantar, Maine Department of Inland Fisheries and Wildlife, personal communication). Despite the risk of MVCs, public input in the management

process does not indicate that the majority of people want to see a large reduction of the moose population along the coast (Morris 2007).

1.4.2.2 New Hampshire

Based on deer hunter surveys and infrared thermal imagery surveys (Bontaites et al. 2000), the 2008 New Hampshire moose population was about 6,000. By 2010 the population was estimated at 4,500 animals (K. Rines, New Hampshire Fish and Game Department, personal communication). Moose densities decreased from north to south in New Hampshire and ranged from 1.2 per km² in the northern third of the state to <0.01 per km² along the more densely human populated coast. Moose numbers were relatively stable throughout most of the state. However, the population appeared to be decreasing in the northern third of the state, as planned under the 2006-2015 New Hampshire Big Game Plan, due to increased hunting pressure and mortality related to winter tick parasitism (K. Rines, New Hampshire Fish and Game Department, personal communication). A recent study in northern New Hampshire (Musante et al. 2007) determined that while cow body weights, survival, and reproduction were high, winterkill-tick infestations in calves resulted in mortality for 24% (14 of 59) of collared calves, accounting for 74% (14 of 19) of calf mortalities. As a result, parasitism rather than factors such as habitat was thought to be limiting the population.

The New Hampshire Big Game Plan 2006-2015 (New Hampshire Fish and Game Department 2005) states the goal for moose management as follows: “New Hampshire will regionally manage moose populations by balancing and incorporating social, economic, public safety and ecological factors, using the best available science.” Management for each of 6 regions in the state seeks to find a balance between the

sometimes incompatible goals of limiting browsing impacts of the resident moose population, maximizing wildlife viewing and hunting opportunities, and limiting MVCs . The management goal for each region varies depending on the priorities in that region, which are determined largely by the public. For instance, limiting MVCs is the priority in the more densely populated southeastern portions of the state, while balancing maximized recreation opportunities and limited browsing impacts is the priority in the north, where lower human population numbers make MVCs not as great a concern (New Hampshire Fish and Game Department 2005). Since 1999, moose hunting permits issued in New Hampshire have ranged from 482-678 in response to changes in observation rates, hunter success, adult sex ratio, fall calf recruitment, and population growth rates, resulting in a legal harvest of between 333-482 moose (K. Rines, New Hampshire Fish and Game Department, personal communication).

1.4.2.3 Vermont

The 2008 moose population in Vermont was estimated at 4,000-5,000 animals, with population densities of 1 per km² in the northeast to ≤ 0.2 per km² in the rest of the state. A 2010 revised estimate of 3,000-4,000 moose statewide reflects the success of the state's management plan to reduce moose density in the northeast portion of Vermont (C. Alexander, Vermont Fish and Wildlife Department, personal communication).

With the initiation of a hunting season in Vermont in 1993 the state desired to stabilize the population in the northeastern portion of the state, where cultural carrying capacity had been exceeded. The stated goals of the plan at the time were to allow for the increase of the moose population throughout the state, with the exception of wildlife management unit (WMU) E in the northeastern corner of the state. In this area, moose

had or were close to exceeding cultural carrying capacity and population stabilization was the goal. Other goals were to monitor the population relative to biological and cultural carrying capacity throughout the state to determine when and if expansion of the hunt was needed, to maximize recreational opportunities derived from the state's moose population, to minimize conflict between humans and moose, and to provide funding for Vermont's Moose Management Program (Alexander 1993).

As the moose population grew throughout Vermont, additional WMUs were opened to hunting and the number of hunting permits increased. Moose hunting is now permitted in most of Vermont. By 2003 the number of permits had reached 440 statewide for a legal harvest of 298 animals. Despite the increase in permits, in the northeastern portion of Vermont the high moose density was causing heavy browse damage, which resulted in declines in body condition and reduction in calving. The number of hunting permits issued in the northeast was increased steadily each year in an attempt to control the population there. In 2004 the number of permits issued was increased to 833. By 2007 the number was 1,250, with 75% of the permits and harvest occurring in the 4 northeast WMUs. In light of trying to reduce the population in this region, half of the permits being issued were for either sex, and the other half were antlerless only (Vermont Moose Management Team 2008a, b; C. Alexander, Vermont Fish and Wildlife Department, personal communication).

In 2008, the continued goals for the state were to further reduce the moose population in WMUs in the northeast (D2, E1, and E2), stabilize the population in most other WMUs, and allow for controlled growth in a few WMUs. It was thought that another several years of high permit numbers would reduce the moose population in the

northeast to acceptable levels, and the subsequent number of moose permits would decrease to around 500 statewide (Vermont Moose Management Team 2008b). Harvest levels in 2009, hunter sighting rates, and a reduction in moose vehicle collisions and non-hunting mortality all indicated that population goals for the northeast WMUs were being met. As a result, permits for WMU D2 were reduced to 90 in 2010, down from 337 in 2009. Permit levels in WMUs E1 and E2 continued to be higher, at 260 and 170, respectively, to further reduce moose numbers in those WMUs, but this too represented a reduction from 600 combined permits in 2009. The Vermont Fish and Wildlife Department expected to further reduce the number of permits in WMU E to 120 in 2011 (C. Alexander, Vermont Fish and Wildlife Department, personal communication; Darling and Alexander 2010; Vermont Fish and Wildlife Department 2010).

1.4.3 Bordering States of Rhode Island, New Jersey, and Pennsylvania

Moose sightings in Rhode Island are still relatively rare, with one or two random reports of a moose every year or so to the Rhode Island Division of Fisheries & Wildlife, normally from north of Scituate. There has never been a report of a cow with a calf. The Rhode Island Division of Fisheries & Wildlife has not had to respond or intervene in a moose incident since the early 1990s when a moose was removed from inside the highway 295 corridor. An attempt was made to relocate the animal to New Hampshire, but the moose died in transit. The Rhode Island Division of Fisheries & Wildlife believes they would receive more sighting reports if there were resident moose in the state; however, they think it is unlikely that the number of sightings they receive could be only from transients (L. Gibson, Rhode Island Division of Fish & Wildlife, personal communication).

There was one report in recent history of a moose crossing the northwest corner of New Jersey; otherwise there are no other reports of moose in the state (C. Condolf, New Jersey Division of Fish and Wildlife, personal communication). Similarly, Pennsylvania had only one report of a young bull in a pasture with female domestic cows in Wayne County, in the northeast portion of the state, about 5 years ago. There have been no other reports of moose in Pennsylvania (B. Wallingford, Pennsylvania Game Commission, personal communication). The lack of activity in New Jersey and Pennsylvania is likely due to the fact that moose are still largely restricted to the upper third of New York and separated from moose in Connecticut by the densely populated areas north of New York City.

1.5 Discussion

1.5.1 Population Trends

Based on the best available estimates, by 2001 the Massachusetts moose population seemed to have stabilized at its current level of about 850-950 individuals. Anecdotal evidence from conversations with MDFW personnel and Environmental Police suggests a decrease in the number of MVCs and occurrences of animals with obvious brainworm symptoms in western Massachusetts, from a peak in the late 1990s and early 2000s. Data on the frequency of moose vehicle collisions and problem moose responses, relocations, and public safety kills in Massachusetts show peaks during 2004-05, followed by a sharp decline (Massachusetts Division of Fisheries and Wildlife, unpublished data). These trends could be attributed to changes in public reporting rates, in personnel in the LART, or in response levels by the LART, but may also reflect a

population trend. The 2010 population estimate in Connecticut of about 75-100 animals may suggest a similar trend toward stabilization. Kris Rines (New Hampshire Fish and Game Department, personal communication) cited a similar trend in southwest New Hampshire. There, moose numbers increased sharply when moose re-colonized and expanded into unoccupied and unexploited habitat. Eventually the population decreased and appeared to stabilize at a slightly lower level. Rines speculated that brainworm could act as a limiting factor once a certain deer density was reached, which then could serve to hold the moose population down.

Moose in Massachusetts and Connecticut are at relatively low densities and viewing moose is difficult due to their tendency to inhabit contiguous forest blocks. Moose carcasses, if found, are often found too late to perform necropsies and determine cause of death. Animals that are afflicted with brainworm or heavy tick loads likely die without symptoms being observed. However, although no cases of brainworm have been confirmed in Massachusetts, no animals have been tested, either. Several cases of brainworm have been confirmed in Connecticut, and many suspected cases have been documented in both states. Winter ticks have been seen on moose captured and observed in Massachusetts; but based on examination of these animals, winter tick infestations were not as severe as in northern New England (Massachusetts Cooperative Fish & Wildlife Research Unit, unpublished data; K. Rines, New Hampshire Fish and Game Department, personal communication; D. Scarpitti, Massachusetts Division of Fisheries and Wildlife, personal communication) or other portions of moose range in North America (Samuel 2007).

Comparison of a Heat Stress Index between a study area in Ely, Minnesota, where Lenarz et al. (2009) found that temperature was affecting survival in moose, to one calculated for central Massachusetts shows that moose in southern New England are subjected to more prolonged periods where ambient temperatures are above thermal neutral zones than in Minnesota. Data from GPS collared moose in Massachusetts show a decrease in use of early successional habitats and a corresponding increase in use of conifer stands and wooded wetlands (Massachusetts Cooperative Fish & Wildlife Research Unit, unpublished data) when temperatures were above the thermal stress temperatures for spring and summer identified by Renecker and Hudson (1986). This indicates that in addition to the expected increased metabolic rates caused by thermal stress, thermal stress may cause moose to perform thermoregulatory behaviors, such as avoiding the best food resources in open habitats, which could lead to declines in body condition and increased mortality in southern New England.

The apparent stabilization of the moose populations in southern New England has come despite observations of high pregnancy rates and occurrence of twins in collared females in Massachusetts (Massachusetts Cooperative Fish & Wildlife Research Unit, unpublished data). Moose are also not hunted in southern New England and the region lacks most predators of moose. Direct impacts of winter tick (Musante 2006), brainworm (Lancaster 2010), and high temperatures (Murray et al. 2006, Lenarz et al. 2009) on the moose population in Massachusetts and Connecticut, factors that have been attributed to moose declines elsewhere on the southern edge of moose range, are difficult to monitor. However, these factors, along with MVCs, likely play a role in mortality of moose in these states. Moose may be at or near the carrying capacity of available habitat in the

deciduous forests of southern New England, but there is no information or even estimates of what densities of moose these forests can sustain. Preferred browse species are heavily browsed in regenerating sites; however, impacts to browse species do not appear to be so great that the vegetation could not sustain more animals.

The irruptive phase of the initial population growth of moose in Massachusetts appears to have ended and data suggest that stabilization may be beginning in Connecticut. The difficulty in accurately estimating moose numbers in the region makes exact determination of population trends difficult, but it appears likely that the population in Massachusetts is declining somewhat from the initial peak after re-colonization. Further information is needed to determine the influence of habitat, parasitism, MVCs, temperature, or other factors on this trend.

1.5.2 Habitat

The long-term future of moose in southern New England is somewhat debatable. It remains to be seen how large a moose population can be sustained in the fragmented, deciduous forests of southern New England and how long-term occupation of the habitat by moose will affect forest plant communities. Preliminary data from the GPS collar study being conducted in Massachusetts suggests that moose are highly dependent on early successional forests resulting from logging. Balsam fir, an important winter food for moose, is not common in most of western Massachusetts and is absent in eastern Massachusetts and Connecticut. In these states eastern hemlock is an important winter browse species for moose. These two main sources of browse, early seral stage forests, and hemlock stands have unknown futures in the region.

In southern New England, where there is a high proportion of small privately-owned wooded parcels, recent studies have shown that logging has been occurring in a shifting mosaic creating an ever-changing pattern of small patches of early successional habitat on these lands (Kittredge et al. 2003, McDonald et al. 2006). Public perceptions of logging in southern New England are often negative. In Massachusetts this has led to pressures to limit or eliminate logging on state lands. In 2010, this pressure resulted in the creation of new forest management plans that greatly reduced the acreage of state land open to logging and limited the types and extent of logging that is permissible. These restrictions place greater demands on private lands to provide early successional habitat in the state, with no guarantees that logging will continue at sustainable levels or that these lands will not be converted or developed. These changes could have obvious negative effects on habitat quality for moose.

Eastern hemlock is threatened with decline due to the hemlock woolly adelgid (*Adelges tsugae*). Outbreaks of hemlock woolly adelgid have already caused widespread mortality of hemlock in Connecticut and elsewhere in the Appalachian Mountains (Orwig et al. 2003). Besides the direct impacts of increased thermal stress, the potential threat of higher temperatures caused by climate change could increase the impacts of woolly adelgid further north in Massachusetts, reducing the distribution of hemlock in the state and limiting an important browse and cover species for moose.

In northern New England habitat does not seem to be the limiting factor it was once thought to be. While early successional habitats in Maine are not at the levels they were after the spruce budworm (*Choristoneura fumiferana*) outbreak of the 1970s and 1980s, the importance of logging to the economy of Maine and the other northern New

England states seems to assure a continued supply of good browse (Morris 2007). As seen in northeastern Vermont, cultural carrying capacity and public safety concerns due to MVCs will likely force wildlife managers to try to keep moose populations at levels below carrying capacity of the habitat. Growing human populations and increased development is a potential limiting factor to growth of the moose population in southern New Hampshire (New Hampshire Fish and Game Department 2005).

Continued human development and urban sprawl, particularly in southern New England and coastal New Hampshire and Maine, may pose the greatest threat to moose in these areas. Direct loss of habitat by conversion of forested lands to development is happening at a rampant rate in Massachusetts (DeNormandie and Corcoran 2009). The combination of loss of habitat to developed areas and increased fragmentation of habitat blocks, with the corresponding increase in risk of MVCs as moose move between habitat patches, is occurring throughout the region.

1.5.3 Management and the Public Role

Throughout the northeast public opinion and involvement in the management process has and will continue to drive moose management policies and population goals. In Vermont, public meetings and public advisory groups composed of members of various stakeholders shaped the management goals and plans for the state when the initial hunting season was being considered. Giving the public a voice in the decision making process and proactive efforts to address the morality of moose hunting likely helped to minimize the anti-moose hunting sentiment that initially existed in the state (Alexander 1993; C. Alexander, Vermont Fish and Wildlife Department, personal communication). Public involvement also plays an important role in moose management in New

Hampshire and Maine as well. Massachusetts' policy for response to problem moose situations was greatly influenced by public sentiment (Vecellio et al. 1993). In New York, public opposition was a significant factor in the decision not to augment the growing moose population in the state (Lauber and Knuth 1997). Public opinion will obviously play a large role in determining if moose are ever actively managed with public hunting in New York, Massachusetts, or Connecticut.

1.5.4 Moose Vehicle Collisions

Throughout the region one of the main concerns regarding moose is the threat to public safety caused by moose vehicle collisions. While relatively rare compared to vehicle collisions with deer and other wildlife, the devastating nature of MVCs and the higher human fatality rate from these collisions makes them a big concern. Increasing moose populations in Massachusetts and Connecticut, two of the most densely populated states in the nation, have led to a corresponding increase in MVCs. Moose vehicle collisions in New York have also increased with the expanding population; however, the distribution of moose in the lightly roaded northern third of the state has limited the number of collisions to date. In northern New England higher moose densities have led to greater numbers of MVCs and related human fatalities, this despite lower human populations and traffic densities (Fig. 1.3).

Since 1996, there have been over 1,000 MVCs annually in the northeastern United States. These collisions have resulted in over 50 human fatalities over the same period, and about 1 out of every 250 MVCs results in a human fatality (Table 1.1; Figs 1.2, 1.3). The 600–700 MVCs per year in Maine alone result in an estimated \$17.5 million in damages (Danks 2007).

Unfortunately, in Massachusetts information on this important issue has become increasingly unreliable and the number of reported collisions has decreased in recent years to 24 and 18 in 2007 and 2008, respectively (Fig. 1.2). This decline is at least partially due to lack of reporting resulting from conflict over ownership of the moose carcass following a collision, a lack of communication among state agencies, and the simple fact that a MVC in Massachusetts is not the novelty it once was. Anecdotal and second-hand reports of moose vehicle collisions now outnumber official reports, and comparison of Division of Law Enforcement and MDFW records indicates only a fraction of MVCs are being reported to MDFW. This decline in collisions may represent an actual trend in the population; however, it is difficult to determine based on current data. By comparison, in 1999 the New York State Legislature amended the law concerning the disposition of moose carcasses resulting from a MVC. This change allows people who accidentally kill a moose with a motor vehicle, and whose vehicle has been damaged, to obtain a permit from a law enforcement officer to keep the carcass (New York State Department of Environmental Conservation 2010). A similar change in the law in Massachusetts may improve reporting of MVCs. Connecticut adopted a law that allows motorists to claim vehicle collision killed deer, moose, and bears in 2008 (H. Kilpatrick, Connecticut Department of Environmental Protection, personal communication).

Research has and continues to be conducted to understand how habitat associations, landscape characteristics, road features, speed limits, moose densities, and traffic volumes influence moose-road interactions. In northern New England, flexible region by region management policies allow for a focus on reducing moose populations

in higher traffic areas to decrease the risk of collisions. In southern New England and New York, state wildlife managers currently do not have this option; they are unable to actively manage the moose herd through hunting to reduce collisions and must rely on signage, public education, and responses to individual problem moose situations to limit the number of MVCs. Moose vehicle collisions will continue to be a concern as long as moose continue to exist in the northeast.

1.5.5 Hunting

The number of moose hunting permits issued in Maine and New Hampshire has ranged over the past decade at about 2,900 and between 400-700, respectively. The number of permits now fluctuates in accordance with changing management goals and changes in moose observation rates, hunter success, adult sex ratio, fall calf recruitment, and population growth rates in the various wildlife management districts in these states. The number of permits issued by the Vermont Fish and Wildlife Department has continued to increase statewide in recent years; however, by far the greatest increase in permits issued has been in the northeastern portion of the state where past management levels failed to achieve the goal of stabilizing and reducing the moose population to below ecological and cultural carrying capacity. Permits issued for the remainder of the state are similar to management levels in Maine and New Hampshire, and the number of permits issued fluctuates with changes in observation rates to meet population goals for WMUs. The current management plan states that another few years of high permit levels in the northeast will reduce the population there, at which point a more conservative management level will be able to maintain moose populations at desired levels (Vermont

Moose Management Team 2008b). The 2010 moose hunting season will see the first such reduction in permits.

The states of Connecticut and New York are exploring the option of managing their moose populations with a hunt; however, in both instances changes in legislation would be required before a hunt is implemented. It remains unlikely that moose will be hunted in Massachusetts in the near future.

1.5.6 Research

Cooperation among state moose biologists and managers in the region is high. An annual meeting takes place for moose managers from all northeastern U.S. states and Canadian provinces to share information and address concerns. Additional meetings and collaborations are being used to create a region-wide method for indexing and estimating moose populations, and a uniform system for classifying moose habitat across the region.

Despite moose being studied extensively throughout their range, important questions remain regarding moose biology, feeding habits, habitat use, life histories, and population dynamics in New England. In southern New England, where information on moose biology, habitat interactions, and forest interactions is scarce to non-existent or anecdotal and speculative, research is currently being conducted to fill these gaps.

Current studies using GPS collars and forest exclosures should provide considerable information in these areas (Wattles and DeStefano 2009, unpublished data). However, applicable and accurate methods to estimate population size and growth, determine causes of and factors influencing mortality and impacts on population growth, and carrying capacity for this unique environment are still being sought (H. Kilpatrick, Connecticut Department of Environmental Protection, personal communication). In

northern New England there is considerable interest in the roles of predation (black bear (*Ursus americanus*) and coyote (*Canis latrans*)) and parasitism (winter tick, lung worm, and brainworm) in limiting moose populations, especially in regards to calf mortality and reduced recruitment rates. A method is being sought to monitor winter tick levels and to determine what levels represent higher than normal mortality. Moose-deer interactions remain a subject for debate, both from the standpoint of interspecific competition for browse and the role of different deer densities on increased levels of parasitism in moose. The impact of moose on forest regeneration is another subject of interest. Managers would like to know what cutting regimes best limit moose impacts on intolerant hardwoods or at what changes in moose density can differences in browse impacts be detected (L. Kantar, Maine Department of Inland Fisheries and Wildlife, personal communication; K. Rines, New Hampshire Fish and Game Department, personal communication).

1.5.7 Management Implications

Moose appear to have a stable future in the region, with populations currently well established in northern New England and relatively stable or growing in Massachusetts, Connecticut, and New York. Concerns over climate change will continue, but moose have to this point shown the ability to adapt to this environment. One of the greatest concerns and challenges for managers in the northeast will be how to manage such a large animal in an increasingly human-dominated landscape.

The return of moose to the northeast is widely heralded as an excellent example of successful wildlife management and natural repopulation of a region by a species.

However, the presence and ecological impacts of such a large, charismatic mammal in

the highly populated northeast raises many questions for researchers and managers. Over the next several years moose will continue to be an interesting topic in the northeastern United States both scientifically and politically.

TABLES

Table 1.1 Human fatalities resulting from moose vehicle collisions in the northeastern United States, 1998-2007.

Year	State						Total
	ME	NH	VT	MA	CT	NY	
1998	5	0	2	0	0	0	7
1999	1	1	1	0	0	0	3
2000	3	2	0	0	0	0	5
2001	1	1	0	0	0	0	2
2002	2	1	1	0	0	0	4
2003	3	1	1	1	0	0	6
2004	4	2	0	0	0	0	6
2005	1	0	1	0	0	0	2
2006	2	0	2	0	0	0	4
2007	5	0	1	1	1	0	8
Totals	27	8	9	2	1	0	47

FIGURES

Figure 1.1 Species range of moose in the northeastern United States, states with moose populations shown in gray, approximate southern edge of species range depicted with dashed line.

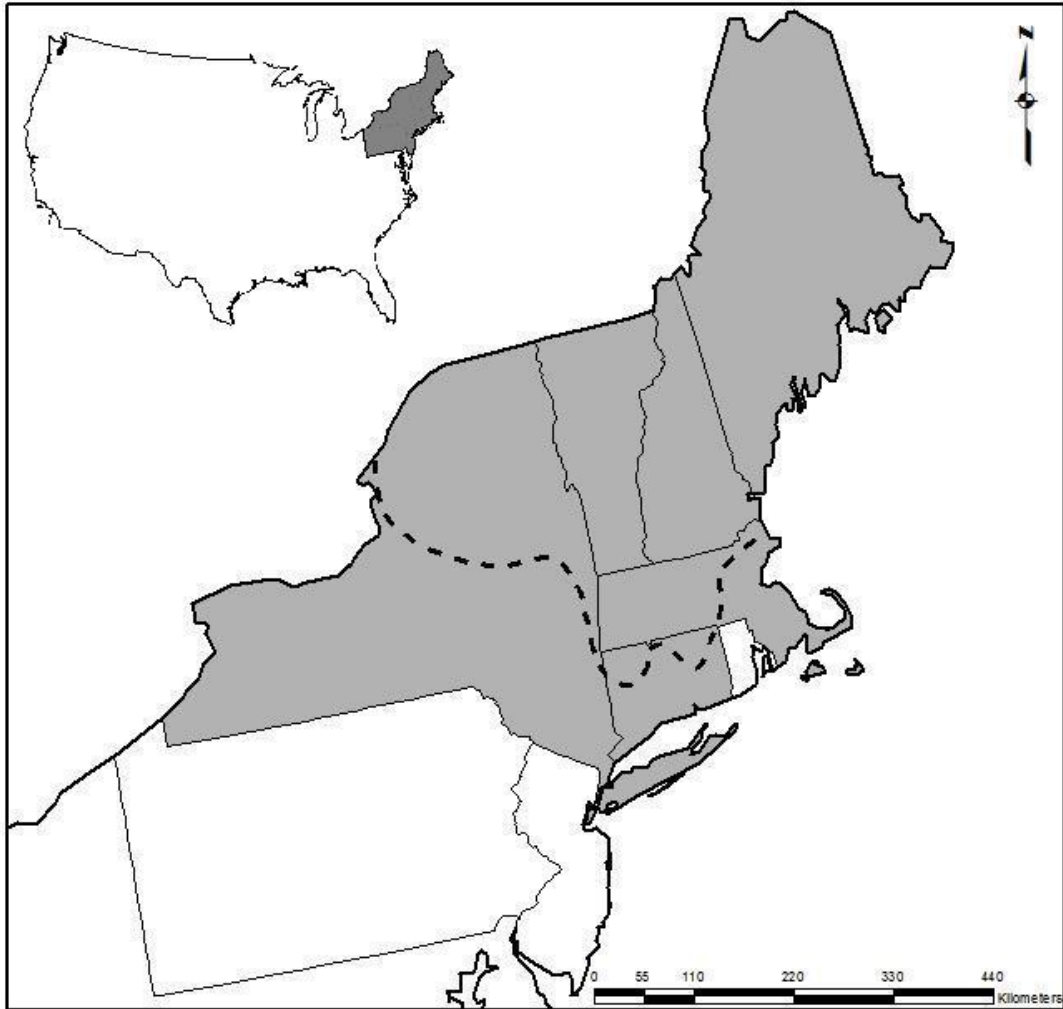


Figure 1.2 Reported moose vehicle collisions in southern New England, 1989-2008.

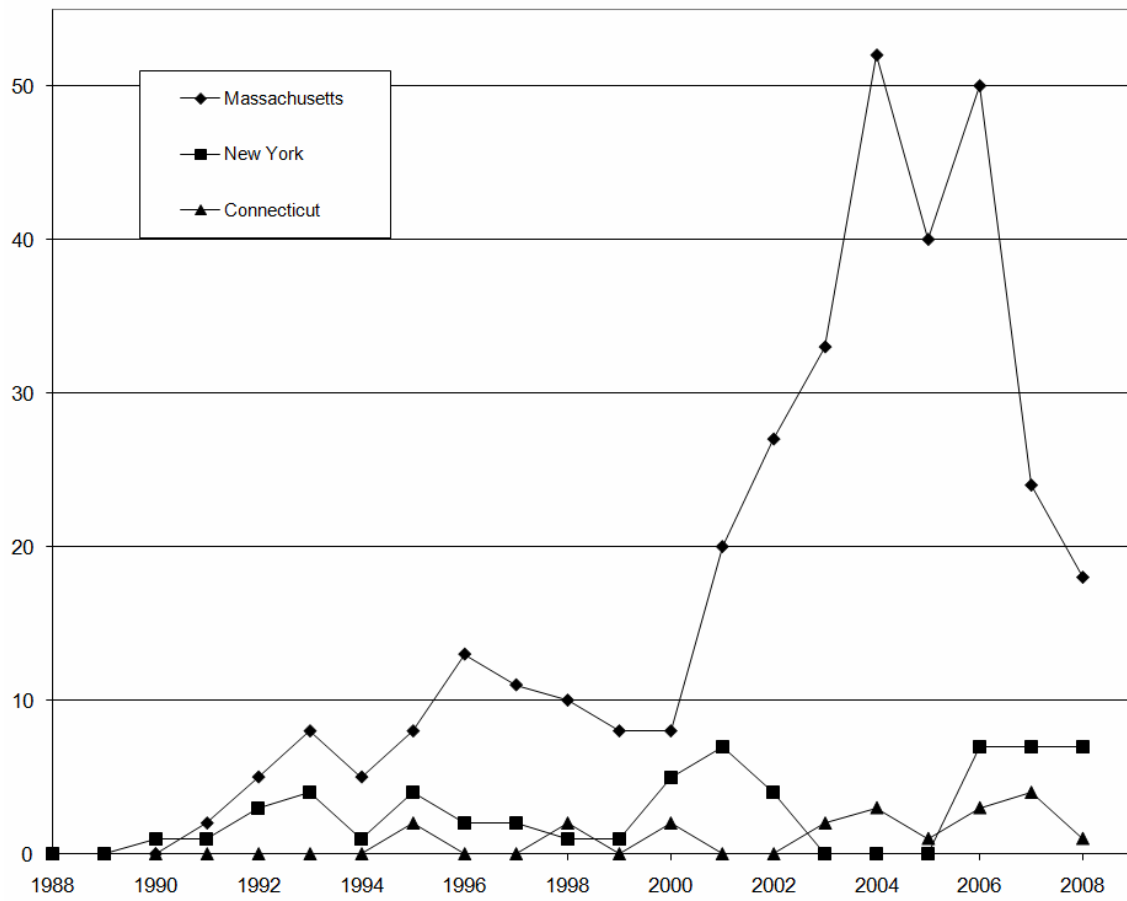
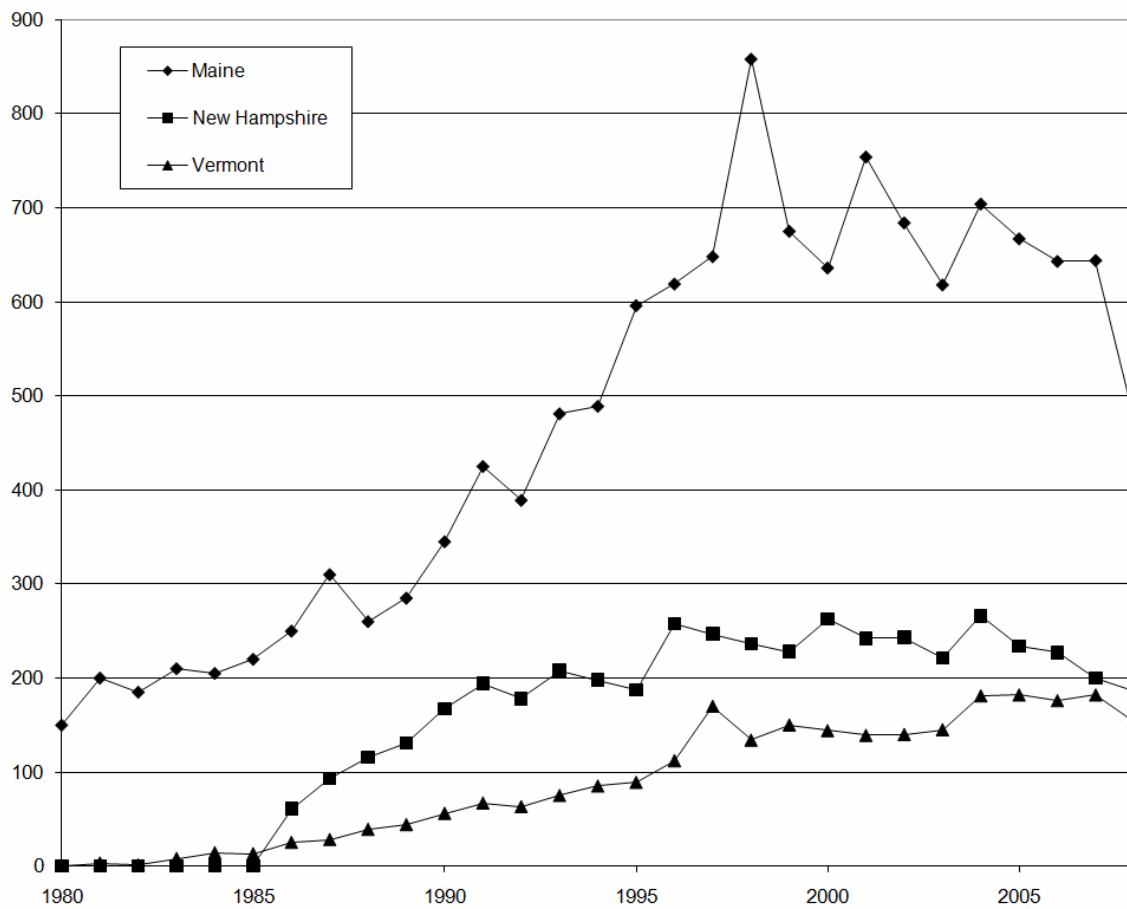


Figure 1.3 Reported moose vehicle collisions in northern New England, 1980-2008.



CHAPTER 2

HOME RANGE, MOVEMENT, AND CORE AREA HABITAT USE OF MOOSE IN MASSACHUSETTS

2.1 Introduction

Burt (1943:351) is given credit for providing the first definition of an animal's home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young". Since then biologists have been attempting to find accurate and meaningful ways of describing animal home ranges, movements, and use of areas within the home range. Where a species can be found geographically, the location of an individual's home range or use of available habitats within the home range is determined by energy constraints. In order for an animal to survive, grow, and reproduce successfully it must have a positive energy balance throughout the year (Hall et al. 1992). An animal's energy balance can be affected by food availability and quality, competition, predation, thermoregulation, parasites, and other factors.

Two of the primary requirements of a home range are to provide the food and the cover an animal requires to meet its annual energy budget. Moose (*Alces alces*) are browsers, feeding primarily on the foliage and twigs of deciduous and evergreen vegetation (Renecker and Schwartz 1997). Moose spend a large proportion of their time foraging and processing (ruminating) the forage, and thus select the vegetative cover types and seral stages that provide the leaves, buds, and twigs in the quantity and quality they need to sustain their large body size (Peek 1997). For many animals, particularly moose and other herbivores in the temperate regions and northern climes of North

America, their annual energy balance is strongly influenced by the seasonal availability of food resources. The availability, quantity, and quality of food that a site provides fluctuates with annual growing and dormant seasons. Throughout the year, changes in moose body condition, feeding rates, metabolism, and activity levels mirror the annual cycles of the vegetation on which they depend (Gasaway and Coady 1974, Schwartz et al. 1984, Regelin et al 1985, Schwartz and Renecker 1997).

The seasonality of resources, created by the growing and dormant seasons for vegetation, results in seasonally positive and negative energy balances for moose. Moose must have a strongly positive energy balance during summer when nutritious vegetation is abundant. This is the time of year when energy stores are replenished and fat layers are deposited for the long dormant season during winter, when catabolism of fat and muscle supplements poorer quality woody and evergreen forage (Gasaway and Coady 1974, Regelin et al. 1985, Schwartz and Renecker 1997). Additionally, during the summer cows and bulls face the increased energy demands of lactation and antler growth, respectively.

Summer or the growing season diet is 1.5-3 times more nutritious than winter diet for moose, resulting in excess digestible energy and protein, compared to a winter diet that is insufficient to meet maintenance needs (Schwartz and Renecker 1997). Moose and other northern cervids greatly increase metabolism, activity, and feeding rates during the growing season, which corresponds to the greater availability of highly nutritious and palatable browse (Regelin et al. 1985, Cederlund 1989, Van Ballenberghe and Miquelle 1990, Schwartz and Renecker 1997). Cederlund (1989) noted a peak in activity corresponding with greatest browse quality at the end of spring to early summer and maximum browse abundance about one month later. Regelin et al. (1985) and Van

Ballenberghe and Miquelle (1990) saw the greatest foraging activity for moose in June.

Van Ballenberghe and Miquelle (1990) suggested that summer is a critical period for moose, when fat and protein reserves can be replenished, which determines how long an animal can survive negative energy balance during winter.

Peek (1997) described the typical annual pattern of moose activity and habitat use that reflects the seasonal availability of resources, and how a moose uses various habitat types on a seasonal basis to meet its annual energy demands. Throughout the year the sites that optimize forage quantity and quality vary and a moose's use of them varies as well. Many factors may cause an individual to deviate from this selection, including avoidance of predators, thermoregulation, snow depth and consistency, rutting and calving, sex, age, population density, and parasites.

In general terms, Peek (1997) described the annual pattern of moose habitat use as follows: (1) use of open uplands and aquatic areas for the forage they provide in early summer, transitioning to closed canopy forests later in the summer as those areas provide the best forage as plant quality changes; (2) after the rut and into winter, intensive use of open areas again, where the highest biomass of dormant shrubs and palatable forage occur; and (3) use of closed canopy patches in late winter, including tall shrub communities and closed canopy conifer forests, as these stands provide not only cover, but also abundant low quality browse when forage availability and quality is at its lowest for the year.

These selection patterns mirror the cycles in moose metabolism, foraging rate, and activity. Moose feeding rates are lowest in mid-winter when browse quality is lowest, at which time they reduce activity and select sites that provide cover to help minimize

energy expenditure (Schwartz et al. 1984, Risenhoover 1986, Peek 1997). Severe winters can exacerbate the restriction on movements. As spring progresses moose shift to sites that provide the highest quality browse, and intensive use of these sites corresponds with periods of highest energy demands for body and antler growth, calving, and lactation (Peek 1997).

Home range size, location, configuration, seasonal and annual overlap and fidelity, areas of concentrated and repeated use, and movement patterns and rates within the home range can provide insights into the seasonal ecology and habitat needs of a species. Johnson (1980) suggested a 4-scaled hierarchy of habitat selection, with each level of the hierarchy dependent upon the previous. Johnson's hierarchy included: (1) first order selection as the selection of the physical or geographical range of a species, (2) second order as the home range of an individual or social group within the geographic range; (3) third order as the use of various habitat or cover types within the home range, and (4) fourth order as the selection and procurement of food items available within the habitat patches. This hierarchy can be used to avoid some of the problems associated with use-versus-availability studies, e.g., when habitat A makes up 80% of the home range and is used 50% of the time, but habitat A is categorized as avoided because it is used less than its availability within the home range. If viewed from Johnson's hierarchy, the second order selection of a home range containing 80% habitat A should be considered selection for that habitat type; the fact that it is used less than available is due then to the super-abundance of habitat A within the home range, not avoidance of it.

Additionally, Retite and Messier (2000) suggested that selection at the coarser scales, including selection of home range within the geographic range, reflects an attempt

to minimize the effects of limiting factors, with more important factors driving behavior at coarser scales. A limiting factor will continue to dominate selection at finer scales until it becomes less important than the next most important limiting factor. Retite and Messier (2000) expected habitat selection would reflect selection for habitats that met microclimate and dietary needs at finer spatial scales (daily selection).

Not all areas of an animal's home range hold equal importance to the animal. If food and other resources are patchily 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 the animal'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.

Moose have recently recolonized a portion of their historic range in southern New England (Vecellio et al. 1993, Wattles and DeStefano 2011), and information is desired on the space requirements, movements, habitat preferences, and habitat use of moose in this region. Space use, movement rates, diet, and habitat requirements for moose have been studied thoroughly throughout much of the species range (Franzmann and Schwartz 1997), including elsewhere in the northeastern United States (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.

Our objectives were to (1) use Johnson's (1980) hierarchy of habitat selection to analyze moose habitat use at multiple scales in southern New England; (2) use minimum convex polygon (MCP) home ranges to define annual and seasonal landscape area requirements for moose in the temperate deciduous forest, and consider how the position and size of MCP home ranges may reflect moose adaptation to limiting factors; (3) use a fixed kernel density estimator (KDE) to quantify habitat use within the larger MCP home range and to identify core area habitats that may be important for moose survival in southern New England; and (4) compare seasonal movement rates and the factors that may influence seasonal movement patterns.

2.2 Study Area

Our study was conducted in central and western Massachusetts, USA (Fig. 2.1), southern New England represents the southern extent of moose range in eastern North America (Fig. 2.2). The central and western sections of the study area are separated by the Connecticut River Valley which runs N-S through west-central Massachusetts.

Topography in the study areas is dominated by glaciated hills underlain by shallow bedrock. Glacial activity has created abundant small stream valleys, lakes, ponds, and palustrine wetlands whose size and nature varies with changes in beaver (*Castor canadensis*) activity. Elevation ranges from 100 m above sea level in the Connecticut River Valley to 425 m in the hills of the central portion of the state, to 850 m in the central Berkshire Hills of western Massachusetts.

Massachusetts is one of the most densely populated states in the U. S. (U. S. Census Bureau n.d.). Development intensity in the upland areas was far lower than the more heavily developed valley floors. In the uplands human development consisted

primarily of isolated homes and homes lining roadways within a matrix of forested habitat. Housing developments were rare in the uplands of the study area compared to eastern Massachusetts and the valley bottoms. There was a dense road network throughout the area, consisting of state highways, paved and unpaved municipal roads, and unpaved forest roads.

In the western two thirds of Massachusetts forests made up >80% of land cover (Hall et al. 2002), with mixed deciduous forests being the climax natural community. Forests were typically regenerating second- or multiple-growth mid-aged mixed hardwoods and conifers, which have resulted from regeneration of farm fields abandoned in the mid-late 1800s (Hall et al. 2002). The forests in the area of Massachusetts used by moose transition across 4 forest types, including spruce-fir-northern hardwood forest, northern hardwood-hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*) forest, transitional hardwoods-white pine-hemlock forest, and central hardwoods-hemlock-white pine forest (Fig. 2.3). 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).

The spruce-fir-northern hardwood forest 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 hardwood forests white pine and hemlock largely replace spruce and fir. The transitional hardwood-white pine-hemlock forests contain most of the species in the forest types to the north and south; in addition oaks (*Quercus* spp.) and hickories (*Carya*

spp.) become increasingly common. The species of the transitional forest type may occur together or in a patchy mosaic depending on site conditions. In the central hardwoods-hemlock-white pine forest, beech, sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*) are rare, replaced by oaks and hickories.

Early successional habitat is created primarily through logging in Massachusetts. While fire, wind, and ice events do create early successional habitat, these events are relatively rare and limited in extent. A significant ice storm did occur in Massachusetts in 2008, which resulted in considerable crown damage in upland forests. This in turn allowed for patches of vigorous growth in the understory. The pattern of logging has been consistent in the study area in the recent past, with 1.5% of the forest area being logged annually, consisting of small (16.5 ha), moderate intensity (removal of 27% of timber volume) cuts created on the landscape in a random pattern (Kittredge et al. 2003, McDonald et al. 2006). The pattern of forest harvest, glaciated landscape, and transitional forest types of the state provides a patchy mosaic of well interspersed forest types, forest age classes, and wetlands.

Massachusetts is a coastal state, and climate is moderated by the Atlantic Ocean. However, temperatures regularly exceeded the thermal neutral zone for moose as identified by Renecker and Hudson (1986) (Fig. 2.4). July is the hottest month with mean high temperatures of 29 and 26 °C and lows of 13 and 14 °C in central and western areas, respectively. January is the coldest month with mean highs of 0 and -2 and lows of -13 and -12 °C in central and western areas, respectively. Mean annual precipitation is 1,073 mm in central and 1,237 mm in western areas, with all months receiving 73-111 mm and 79-123 mm, respectively. 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 depths are typically greater in western Massachusetts than central areas and can reach the depths identified by Coady (1974) that restrict moose movement (>60 cm) (Fig. 2.5).

In central Massachusetts, initial deciduous bud-break for red and white oak (*Quercus rubra* and *Q. alba*), red (*Acer rubrum*) and striped maple (*A. pensylvanicum*), yellow birch, and common witchhazel (*Hamamelis virginiana*) is late-April to early-May. About 75% leaf out of the deciduous canopy occurs in late-May to early-June, and about 50% loss of the deciduous canopy occurs by mid to late-October (O’Keefe 2000). Forest canopy closure in the deciduous forest is nearly 100% under leaf-out conditions.

2.3 Methods

2.3.1 Capture

We captured moose by opportunistically stalking and darting them from the ground or collaring and relocating moose from problem animal situations, between March 2006 – 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 5 cc or 3 cc Type C Pneudart dart (Pneudart, Inc., Williamport, PA, USA). The 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 possibly 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 minutes. Collars were equipped with very high frequency (VHF) transmitters, mortality sensors, and automatic release mechanisms that released the collars either at a low battery state or a preprogrammed date.

2.3.2 Home Ranges

We used both MCP (Hayne 1949) and KDE (Worton 1989) home range estimators to describe moose home ranges. Harris et al. (1990) recommended using at least 2 home range estimators for all animal location data sets, 1 of which being the MCP due to its prevalent use and relative comparability. We used MCPs to describe landscape level space use of moose and KDEs to quantify use within those home ranges. We calculated 100% MCP home ranges using the Create Minimum Convex Polygons tool in Hawth's Analysis Tools (Beyers 2007). We created utilization distributions (UD) using the fixed kernel setting in Kernel Density Estimation tool in HRT: Home Range Tools for ArcGIS (Rogers et al. 2007). All Geographic Information System (GIS) work was performed in ArcGIS 9.3 (ESRI 2008).

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 more precise but also more biased UD that encompasses unused habitats, while a small h under-smooths the data, resulting in a fragmented UD (Fieberg 2007) .

Powell (2000) recommended least-squares cross validation as the best method for calculating the smoothing parameter using the data. However, Hemson et al. (2005) demonstrated the method often fails when confronted with clustered and large data sets

(as with GPS collar data), causing h to approach zero. As a result many software programs often fail to create a UD using this method. Gitzen et al. (2006) discussed other methods for determining h , including using the reference bandwidth (h_{Ref}) or some proportion of it, but found that no method works best for all distributions and sizes of data sets. Despite finding the least-squares cross validation method of determining h unsatisfactory, Hemson et al. (2005) failed to find a stable relationship with factors of h_{Ref} and sample size or other variables that would make it a reliable option. Fieberg (2007) also showed that differences in sample size can affect the calculated value of h_{Ref} . We encountered similar problems using h_{Ref} , with the distribution of the data points having a large effect on the calculation of h_{Ref} , i.e., dispersed data resulting in large h_{Ref} values compared to more clumped data, making comparisons of KDE home ranges calculated with this method impossible.

To define a continuous home range with a KDE, Kie et al. (2010) suggested using successive proportions of h_{Ref} until the UD merges into a single polygon. However, Mitchell and Powell (2008) showed that KDE can perform poorly in landscapes that are fragmented or have a patchy distribution of resources when a large h is used to calculate the UD. They stated that the UD should fragment into multiple polygons in these types of landscapes, more accurately representing the patchiness of resources and separate used and unused habitats in the UD, and therefore a small h should be used. The forested landscape in Massachusetts, and moose use of it, is patchy and highly fragmented due to the extensive road network, irregular distribution of early succession habitats, small wetlands, and heterogeneous forest types. Therefore, use of a small h that results in fragmented UDs is desirable to accurately represent habitat use. A small h would thus

identify used patches and exclude unused areas. However, if the goal is to define a home range using KDE methods, a balance must be reached between merging the resulting UD into one or several clumped polygons and over-smoothing the UD and positively biasing the home range. Wand and Jones (1995:57) stated “There are many situations where it is satisfactory to choose the bandwidth subjectively by eye”.

Due to the lack of agreement on the best method and unreliability of quantitative methods for calculating h , we chose a 200-m bandwidth for use in calculating KDE home ranges. We selected the 200-m bandwidth to strike a balance between creating a continuous home range polygon and over-buffering the outer edges of the home range. The 200-m bandwidth value merged closely separated locations into a single polygon, but failed to merge widely spaced clusters of locations together. Increasing the bandwidth beyond 200-m resulted in greater bias of home ranges by increasing the buffer around all points, but failed to further merge disjointed polygons into a single home range unless very large values of h were used. Smaller values of h resulted in more fragmented UDs that did not reflect a KDE home range.

2.3.3 Core Area Habitat Use

Having already defined home ranges by using MCP and KDE methods, we used 2 smaller values of h to minimize over-smoothing biases to calculate UDs that represented habitat use. First, to identify home range cores, we used a bandwidth of 80-m, a value that began to combine disjunct but narrowly separated portions of the UD into single polygons, but still allowed for fragmentation of the utilization distribution across roads and more widely spaced clusters of locations. The 50 percent isopleths of the 80-m UD was used to identify home range cores. However, the 80-m bandwidth still resulted in

over-smoothed UD's 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 UD's incorporated little unused habitat and were used to assess habitat use within core areas.

We classified habitat use into 19 categories that we later compressed into 8 categories (Table 2.1). A GIS baselayer for Massachusetts that accurately maps forest type, successional stage, and other habitat classifications does not currently exist. Therefore, we manually digitized habitat within the cores in ArcGIS 9.3 (ESRI 2008) using a compilation of available baselayers from MassGIS (MassGIS 2011) and other sources, including 2005 and 2009 orthophotos, Massachusetts Department of Environmental Protection wetlands layers, forest harvest information from the Massachusetts Department of Conservation and Recreation and Harvard Forest (McDonald et al. 2006), and 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.

2.3.4 Habitat Availability and Biological Season

We generated sets of 250 random points within 100% annual MCPs using the Generate Random Points tool in Hawth's Tools (Beyers 2007). We assessed habitat availability by manually classifying the habitat where the 250 random points were located. We saw little difference in available habitat classified with 250, 500, 750 or 1,000 random locations for several home ranges, so we used 250 locations for the remainder of the home ranges.

We defined the length and timing of seasons based on several ecological factors: these included timing of the growth and dormant seasons of vegetation and resultant changes in availability and quality of browse; weather, including temperature and snow conditions; and seasonal influence of the moose reproductive cycle (Table 2.2). The transition between seasons can vary by a period of several days to several weeks depending on weather conditions and timing of leaf-out or leaf-off, or beginning of a biological period. 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 associated with spring movement 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.

2.3.5 Movements

We calculated mean and median seasonal daily movement rates for moose by calculating the distance between successive fixes and summing those distances for each 24-hour period beginning at 0:00. We then averaged the 24-hour totals across seasons for each animal, then across animals (e.g., all males in the western study area). 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 movement path. We corrected for the variable sampling rate in our collars (135, 75, and 45 min) by subsampling the more intensively sampled datasets, taking every other and then every third location, and simulating the longer sampling intervals of the 135-minute fix interval collars. We then calculated movement parameters as before and compared the results. We saw consistent reduction in movement rates with increasing sampling interval. Therefore,

we used the proportional seasonal change in movement rate to scale the movements observed in our 135- and 45-minute collars to the 75-minute sampling level.

2.3.6 Statistics

We used analysis of variance (ANOVA) to analyze the differences in seasonal home range size, movement rates, habitat availability, and core area habitat use within and between groups. 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. Due to the high variability of biological data and thus limited power, we set the significance level at 0.1. All statistical analyses were performed using the open source software R, version 2.12.2 (R Development Core Team 2005).

2.4 Results

2.4.1 Capture and Deployment of GPS Collars

We deployed 45 GPS collars on 35 moose (14 females and 21 males). Ten moose were recaptured and recollared when the batteries in their initial GPS collars ran low. We only included free-ranging moose in this paper due to uncertainty regarding home range and movement data from relocated moose. Of the 25 free-ranging moose, we excluded 2 from analysis due to suspected moose sickness (infection with the parasite *Parelaphostrongylus tenuis*) and mortality. In addition, collars on 3 animals failed resulting in inability to retrieve the collar or no acquisition of data. Nineteen moose are included in this analysis: 5 females (all in central Massachusetts) and 14 males (7 in central and 7 western Massachusetts) (Table 2.3). Seasonal data for any animal was only

included in the analyses if data were obtained across the entire season (see Table 2.2).

We obtained 122,713 locations of the 19 moose used in this study, with an overall fix rate of 84.5% (Table 2.3). The median number of locations 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.

2.4.2 MCP Home Ranges

Mean annual MCP home range sizes were not different for male (73.3 km²) and female (64.9 km²) moose in central Massachusetts ($P = 0.98$; Table 2.4). However, western males had larger annual home ranges (164.5 km²) than either central males or females ($P = 0.038$ and 0.037 , respectively).

Seasonal MCP home range size for females in central Massachusetts ranged from 23.0 km² during fall and 23.8 km² in early winter, to 39.2 km² during summer. Differences in seasonal home range size were not significant ($P \geq 0.47$). Seasonal MCP home range size for males in central Massachusetts ranged from 24.1 km² in summer and 25.0 km² in late winter, to 41.9 km² during fall, with no significant differences in size ($P \geq 0.35$). In western Massachusetts, MCP home ranges for males varied from 19.2 km² in late winter to 214.9 km² during fall, with fall home ranges significantly larger than all other seasons ($P \leq 0.015$).

Mean seasonal MCP home range sizes were not different for male and female moose in central Massachusetts ($P \geq 0.31$). Male moose in western Massachusetts had larger fall home ranges than either males or females in central Massachusetts ($P = 0.020$ and 0.022 , respectively).

Median annual and seasonal MCP home ranges sizes were often smaller than the means (Table 2.4). Median female summer home range size (31.2 km^2) was 8 km^2 smaller than the mean (39.2 km^2). For males in central Massachusetts, median early winter, late winter, and annual home ranges were 9, 5.4, and 15.1 km^2 smaller than the means, respectively. For western males the greatest differences between median and mean home range size was in spring and fall, and also in annual home ranges (14.1 , 100.9 , and 60.9 km^2 , respectively).

2.4.3 Kernel Home Ranges

Mean annual KDE home range sizes were not different for western males (35.2 km^2) or male (25.4 km^2) and female (26.7 km^2) moose in central Massachusetts ($P \geq 0.36$; Table 2.5).

Seasonal KDE home range size for females in central Massachusetts ranged from 11.9 km^2 during fall and 12.0 km^2 in early winter, to 17.3 km^2 during summer, with no significant differences in size among seasons ($P \geq 0.18$). Seasonal KDE home range size for males in central Massachusetts ranged from 9.9 km^2 in late winter to 18.7 km^2 during fall. Differences in seasonal home range size were not significant ($P \geq 0.53$). Seasonal KDE home ranges varied from 7.4 km^2 in late winter to 29.8 km^2 during fall for males in western Massachusetts, with fall home ranges significantly larger than all other seasons ($P \leq 0.08$). Additionally, spring KDE home ranges (19.3 km^2) were larger than late winter ($P = 0.010$).

Mean seasonal KDE home range sizes were not different for male and female moose in central Massachusetts for any season ($P \geq 0.22$). Male moose in western Massachusetts had larger KDE home ranges than those of central females in late winter,

spring, and fall ($P \leq 0.061$) and larger home ranges than central males during fall ($P = 0.018$).

2.4.4 Movements

Daily movement rates for female moose in central Massachusetts were consistently around 1,000-1,500 m/day from the beginning of the year until late April, at which point they nearly doubled to close to 3,000 m/day prior to calving (Fig. 2.6). There was a sharp decline in movement rates to 500 m/day on 11 May, the mid- point of the observed 8-13 May calving period. Mean daily movement rates remained low for May and most of June, increasing slowly as June progressed, before peaking around 3,000 m/day in early July and remaining high for the remainder of the summer. Movement rates declined in September by about 1,000 m/day from the summer high and remained fairly consistent for the rest of the year.

Daily movement rates were lowest (1,000 m/day) for central males from the beginning of February until the end of March (Fig. 2.7). Movements began increasing early in April and peaked at around 2,500 m/day in late-May and early June, before reducing slightly during summer. A further reduction occurred in late summer, during the warmest period of late July through August. An increase in movement indicating the start of the rut began in early September, first reaching 3,000 m/day during the second week of September, then increasing to a peak of nearly 8,000 m/day the last week of September. Movements remained extremely high until the first week of October when a sharp decline was seen. Daily 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.

Western area males had similar daily movement rates to males in central Massachusetts (Fig. 2.8). Annual lows in daily movement were 1,000 m/day or less from the beginning of February until early April, when movements increased by 1,000 m/day or more. Movement rates during this period showed a slight peak in late May to early June, then remained around the 2,000 m/day level until July and August, when movement rates were slightly lower. Movements associated with the rut began in early September, sharply increasing to >4,000 m/day in mid-September and remained high until an abrupt drop off in early October. Daily movement rates declined from this point until settling around 1,500 m/day by early December.

Seasonal scaled mean daily movement rates for female moose in central Massachusetts were greatest during summer (2,509 m/day) and lowest during the calving season (874 m/day) (Table 2.6; unscaled movement rates are presented in Table 2.7). Summer movement rates were greater than all seasons except spring ($P \leq 0.06$). Spring pre-calving movement rates were also greater than those in early winter, late winter, and calving season ($P \leq 0.007$). Fall movement rates were greater than during calving season ($P = 0.006$). Daily movement rates for male moose were greatest during fall (3,451 and 3,464 m/day for central and western males, respectively) and lowest in late winter (1,310 and 1,064 m/day, respectively). Fall movement rates for male moose in central Massachusetts were greater than all other seasons ($P \leq 0.007$), and greater during both spring ($P = 0.025$) and summer (0.089) than late winter. Similarly, movement rates for male moose in western Massachusetts were greater in fall than all other seasons ($P \leq 0.012$), and greater in spring than in late winter ($P = 0.042$).

Fall daily movement rates were lower for females than males in both central ($P = 0.049$) and western (0.040) Massachusetts. However, females had greater movement rates than either group of males during later winter ($P = 0.063$ and 0.020 for central and western males, respectively).

2.4.5 Location and Composition of MCP home ranges

All moose KDE home ranges were located on the uplands in both central and western Massachusetts. Very limited use of valley bottoms was observed. When valley bottom was included in a MCP home range it most often was unused habitat or an area that was merely traversed in movements between ridge tops.

Both MCP and KDE home ranges of moose were dominated by forest cover and wetlands. MCP home ranges consisted of 84% (73–93%) forested cover types and 12% wetland cover types (4–23%). KDE home ranges were 88% (78–95%) forested, with 9% (3–16%) made up of wetlands. Home ranges with lower amounts of forest cover were those with the greatest amount of wetlands.

All types of roads were at lower densities within KDE home ranges than either (1) the overall MCP home ranges or (2) the area outside the KDEs but within the MCPs, with the exception of forest roads (Table 2.8). The higher density of forest roads in KDE home ranges was due to the large proportion of state forests, wildlife management areas, and other conservation areas, where forest roads occur, in KDE home ranges. The areas outside the KDE but within the MCP home ranges had higher densities of all developed road types than either the MCP as a whole or the KDE, indicating that moose were avoiding the areas of their MCP home range that had higher road densities and higher levels of development.

Conservation land made up 59 and 69% of MCP and KDE home ranges, respectively, for moose in Massachusetts. Amount of protected land varied from 37-96% in MCP home ranges and from 23-98% of KDE home ranges.

2.4.6 Habitat Availability

There were no significant differences in availability of vegetative cover types for males and females in central Massachusetts ($P \geq 0.13$; Fig. 2.9). There was, however, a greater proportion of deciduous forest (0.21) in western male MCP home ranges than either males (0.13; $P = 0.052$) or females (0.11; $P = 0.020$) in the central part of the state. Western male home ranges had less mixed forest (0.24) available to them than central females (0.30; $P = 0.066$). Central males had more regenerating forest (0.30; $P = 0.034$) and other wetlands (0.11; $P = 0.080$) available to them than did western males (0.21 and 0.05, respectively).

2.4.7 Home Range Core Area Habitat Use

Regenerating forests made up the largest proportion of female moose home range core areas during all seasons (0.48 during spring to 0.59 in late winter), and was significantly greater than all other cover types for all seasons, with the exception of wooded wetlands and mixed forests during spring (Spring: $P = 0.056$, 0.007, and 0.006, for conifers, deciduous, and other wetlands, respectively; Summer, Fall, and Late winter: all $P < 0.001$; Early winter: $P = 0.003$, 0.025, 0.015, <0.001 , and <0.001 , for conifers, deciduous, mixed forest, other wetlands, and wooded wetlands, respectively) (Fig. 2.10). No other differences in seasonal core area habitat use were significant for females. Similarly, the proportion of central male moose home range cores composed of

regenerating forests was greater than all other habitat types for all seasons (0.43 during spring to 0.68 during late winter) (Spring: $P = 0.025, 0.042, 0.007, 0.078$, and <0.001 for conifers, deciduous, and mixed forests, wooded wetlands, and other wetlands, respectively; Summer, Fall, and Late winter: all $P < 0.001$; Early Winter: $P = 0.001, 0.027, <0.001, <0.001$, and <0.001 , for conifer, mixed, and deciduous forest, wooded wetlands and other wetlands, respectively) (Fig. 2.11). Wooded wetland use was greater than mixed forests during fall ($P = 0.054$).

For males in western Massachusetts the importance of vegetative cover type varied with season, with deciduous forest making up the greatest proportion of home range cores in spring (0.41), regenerating forests during summer (0.56) and fall (0.38), and forest types with a conifer component (mixed and conifer forests) combining to be the most heavily used in early (0.48) and late winter (0.63) (Fig. 12). In western Massachusetts, male moose used deciduous forests more than all habitat types except regenerating forest during spring ($P = 0.002, 0.013, <0.001$, and <0.001 , for conifers, mixed forests, other wetlands, and wooded wetlands, respectively). Regenerating forests were also used more than other wetlands during spring ($P = 0.062$). During summer regenerating forests use in home range cores was greater than all other habitat types (all $P < 0.001$). Fall use of regenerating forest was greater than conifer forests and other wetlands ($P = 0.077$ and 0.063). In early winter conifer forests made up a larger proportion of home range cores than wooded and other wetlands ($P = 0.012$ and 0.022), and regenerating forests were used more than wooded and other wetlands and deciduous forest ($P = 0.002, 0.003$, and 0.045 , respectively). During late winter conifer and mixed forests both made up more of home range cores than wooded wetlands ($P = 0.051$ and

0.003 for conifer and mixed forests, respectively) or other wetlands ($P = 0.032$ and 0.002 for conifer and mixed forests, respectively). Mixed forests were also used more than deciduous forests ($P = 0.089$).

Other wetlands made up a greater portion of female seasonal home range cores during summer than early winter ($P = 0.096$). There were no other differences in the use of various vegetative cover types by females between seasons. Males in central Massachusetts had a greater proportion of mixed forest in their early winter than fall home range cores ($P = 0.035$), more wooded wetlands in spring cores than late winter (0.080), and more other wetlands during fall than early winter (0.094). Western male moose had greater seasonal variation in their use of vegetative cover types. Males in western Massachusetts used more conifer forest in their early winter home range cores than during spring, summer, and fall ($P = 0.042$, 0.035 , and 0.034 , respectively), and a greater proportion of conifer during late winter than summer and fall ($P = 0.079$ and 0.071). Regenerating forests were used more by western males during summer than spring ($P = 0.083$) or late winter ($P = 0.032$). Western males had more mixed forest in their late winter cores than summer ($P = 0.015$), while use of deciduous areas was greater during spring than early or late winter ($P = 0.033$ and 0.062). Wooded wetland use was greater during fall than early and later winter and spring ($P = 0.006$, 0.007 , and 0.073 , respectively).

There were no differences in seasonal core area habitat use between males and females in central Massachusetts (Figs. 2.13-2.17). However, males in western Massachusetts used deciduous forests more than females or males in the central part of the state during spring and fall (Spring: $P = 0.003$ and 0.032 ; Fall; $P = 0.017$ and 0.012 ,

for females and males, respectively). Conifer forests also made up a greater proportion of western male home range cores than central females during early winter ($P = 0.014$) and more than central males during both early and late winter ($P = 0.037$ and 0.071). Males in the western part of the state also used mixed forests more than central males during late winter ($P = 0.027$), but regenerating forest made up a smaller portion of their late winter cores than both central females and males ($P = 0.015$ and 0.002).

2.4.8 Use Availability Ratios

During spring female moose had selection ratios (proportion of use in their home range cores : proportion available in MCP) greater than 1 for regenerating stands and wooded wetlands, indicating selection of these cover types during spring (Fig. 2.18). Males in central Massachusetts showed a strong preference for wooded wetlands during spring, with a selection ratio of 4.75, but also had a selection ratio >1 for conifer, deciduous, and regenerating forests (Fig. 2.19). Western Massachusetts males showed the strongest selection for deciduous stands, with use in cores almost twice as much as available, but also showed selection for regenerating stands and wooded wetlands (Fig. 2.20).

In summer all 3 groups had selection ratios >1 for regenerating forests and wooded wetlands. Males in the west also showed selection for other wetland types. Most other cover types were used less than available, but were likely very important as thermal cover habitat for moose.

Regenerating stands and wooded wetlands were both used more than available by all 3 groups during fall. Males in western Massachusetts showed their strongest selection

for wooded wetlands during fall. Western males used deciduous stands more than available.

In early winter regenerating stands were used more than their availability by all 3 groups. Females used deciduous more than available, while males in central Massachusetts increased their use of conifer and mixed stands close to what was available. Males in western Massachusetts showed selection for conifer stands. In late winter males in western Massachusetts further increased their selection of conifer and mixed stands and used regenerating stands less than their availability for the only period of the year. Central Massachusetts moose showed increased selection for conifer as winter progressed and continued to use regeneration more than available.

2.4.9 Behavior and Timing of Calving and the Rut

Female moose began concentrating their habitat use at their calving site between 8 May and 13 May ($n = 6$ females for 7 seasons), with one exception. One cow did not concentrate her habitat use at one location during the calving season, but small concentrations of GPS locations indicated a calf was born around 30 May. This female was seen with a calf later in the summer. The delay in birth of this calf was possibly due to fertilization during a second estrus period, which is probable given the more isolated area where the female's home range was located. For the remainder of cows, habitat use remained concentrated near the calving site until the end of the second week of June. Calving sites varied among individuals and included wooded wetlands, mature mixed and conifer-dominated mixed stands, and mixed and conifer shelter cuts.

Changes in movement patterns for bulls indicating the initiation of the rut was variable and included large increases in daily movements, movements outside of the

summer range, movements to a specific fall range, repeated movements that covered the length or width of the home range, movements back and forth between multiple centers of activity, and wide-ranging movements outside of the remainder of the animal's home range. Timing of the initiation of these behaviors also varied, but began as early as the last few days of August or as late as the last week of September. The peak of these movements was between the second week of September and the first week of October. The maximum single daily distance moved was 25.5 km, but typical peak daily movements were 6-10 km.

2.5 Discussion

2.5.1 Home Range

Home range size can indicate the area of the landscape required by an animal to meet its needs of food, cover, water, and reproduction, but can also reflect limitations imposed on movements by snow depth, thermoregulation, or other factors. Powell (2000) suggested that animals have a cognitive map of their home range and the distribution of cover types and resources within it. As such, an MCP home range represents not only landscape scale space use by an animal, but also the area of the landscape known to the individual. Different areas may or may not receive use in any given time period or year, may receive use in one period but not again for some time, or may simply be traversed when moving between 2 habitat patches. Because an area was not observed to be used during the period of study does not mean it will not be used in the future or is not important to provide connectivity. For example, the annual MCP home range of one bull that was collared for 3 years changed little in that time, but areas of use within it changed

annually, particularly during winter. Patches of mixed forest or shelter harvests that were used intensively one winter were not used in subsequent years, while other areas not used the first year became winter cores areas in following years; still other areas never received use. Similarly, as new areas of forest regeneration were created through harvest within the home range, a section of forest that received little use could become an important resource patch as regeneration progressed. The general patterns of use of vegetative cover type changed little year to year, but the specific patches that were used could change considerably.

Home range size, particularly for MCPs, can be greatly influenced by outliers or a movement to and use of an area away from the center of the seasonal or annual home range. Alternatively, utilization distributions created by the fixed KDE method describe the pattern and intensity of areas of use within the MCP home range. If used habitat patches are widely spaced, the resultant UD created with a small smoothing parameter will fragment into multiple patches. The KDE home range can also be used to differentiate the intensity of use of various areas by examining different isopleths of the UD. By examining both MCP and KDE home ranges, we can distinguish the area of the landscape used by an animal to find all the habitat patches or mates it required for a time period (the MCP home range) as well as the areas of actual use and the relative intensity of use of those areas (the KDE home range).

In this study, median annual MCP home range sizes of 58.2 and 60.6 km² were similar for males and females, respectively, in central Massachusetts. The large annual home range size of males in western Massachusetts (103.6 km²) was due to the influence

of several animals with portions of their home ranges on ridge tops separated by unused valley bottoms, as well as large movements during the rut by young bulls.

Female moose MCP home ranges were largest during summer (27.9 km²), which corresponded to the period of greatest energy demands from lactation, the need to restore their body condition for survival of the coming winter, and gestation during the following spring. Males in both portions of the study area had their largest seasonal home ranges during fall (37.3 km² central and 114.0 km² west) when they were searching for and attending to mates during the rut. The higher proportion of young males collared in western Massachusetts may explain the larger fall home ranges compared to males in central Massachusetts. Males in both central and western Massachusetts had small home ranges during late winter (19.6 km² central and 18.8 km² west) when home range size was likely restricted by lower metabolism and snow conditions, and during the summer (20.3 km² central and 28.2 km² west) when thermoregulatory constraints played an important role.

Despite the large number of studies on moose home range size (Hundertmark 1997), it was difficult to compare our results with many of these studies. Most studies were carried out using traditional VHF telemetry and home ranges were calculated using a small number of locations (e.g., <30), particularly in winter (<10). Low numbers of telemetry locations have the potential to underestimate home range size. In addition, in many studies few VHF locations were collected at night when moose can be active. Kernohan (2001) suggested 30 as a minimum number of locations, but that at least 50 locations should be used to calculate an accurate home range. Additionally, differences in

method of home range calculations and the length, timing, and number of seasons used in the study can make comparisons difficult.

In the northeastern United States, our results compare well with those of Leptich and Gilbert's (1989), who had >50 locations for 11 of 13 collared moose and estimated a summer MCP home range of 25.2 km² for females in Maine. Also in Maine, Thompson et al. (1995) reported median summer home ranges of 32.3 km² for females and 28.0 km² for males, but mean number of observations for all other seasons were too low for comparison. Thompson et al. (1995) did note that winter ranges were typified by concentrated use in small areas (<2 ha), with movements of <1 km to other areas of intensive use, which is similar to what we observed. In northern New Hampshire, Scarpitti et al. (2005) observed smaller seasonal home ranges for females than our study (≤ 17.4 km² for all seasons). An earlier study in northern New Hampshire by Miller and Litvaitis (1992) reported much larger annual home ranges for females (152.9 km²), with the largest seasonal home ranges during fall (81.7 km²). Garner and Porter (1990) reported 36.3 km² for summer and 7.5 km² for winter home ranges of males in the Adirondack Mountains of New York.

Our results fall within the range presented by Hundertmark (1997) in his summary of moose home range size across North America. A study in northeast British Columbia of female moose with GPS collars had larger annual and seasonal MCP home ranges than what we observed in Massachusetts (annual 195.28 km², calving 17.59, summer 60.25, fall 46.85, winter 45.91, late winter 30.49) (Gillingham and Parker 2008). However, Gillingham and Parker also observed that female summer home ranges covered the largest areas during the year. The much larger annual home ranges in British Columbia

could be related to movements across elevation gradients in mountainous terrain, which may be similar to what we saw with disjointed upland home ranges separated by valley bottoms. Dussault et al. (2005) observed that home range size was highly variable in Quebec, particularly in summer, and found larger home range sizes and movement rates for both males and females during summer than winter, but the difference was significant only for females.

2.5.2 Habitat Use

Peek (1997) described the pattern of annual moose activity and habitat use that reflects seasonal availability of resources. Moose will use a variety of cover types to meet their annual energy demands. Throughout the year sites that provide optimal forage quantity and quality vary, and their distribution on the landscape affects the seasonal movements and habitat use of moose. Many factors may cause individual animals to deviate from this pattern of habitat selection, including avoidance of predators, thermoregulation, snow depth and consistency, rutting and calving, sex, age, population density, and parasites.

Any description of the pattern of annual moose habitat use and activity is also influenced by the spatial scale of the analyses, and many authors suggested that habitat use and selection be examined at multiple scales (Johnson 1980, Wiens 1989, Nikula et al. 2004, Osko et al. 2004). Within an established geographic range of a species (Johnson's first order), Johnson (1980) stated that selection starts with the home range. As such, the placement and composition of the home range represents the highest order (second order) selection of habitats within the geographic range.

In Massachusetts, moose home ranges were almost exclusively located on the uplands of the central and western parts of the state. By positioning their home ranges on the less developed uplands, using state lands and other conservation areas, and using areas with lower road densities, moose appeared to be selecting 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. Use of higher elevations could also be an attempt to limit thermal stress by taking advantage of reduced ambient temperatures and increasing 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. Rettie and Messier (2000) argued that selection at the scale of the home range can reflect attempts to reduce the effects of limiting factors.

2.5.3 Use of Core Areas

The scale that is more typically addressed in habitat use studies is stand or patch scale selection (Aebischer et al. 1993, Alldredge et al. 1998, Manly et al. 2002). The seasonal changes in vegetation associated in dormant and growing seasons for plants determines the availability and quality of available food resources and the vegetative cover types that moose select. In Massachusetts, the beginning of the vegetative dormant season occurred at the end of October and beginning of November and represented the transition from moose consuming primarily green vegetation to woody and evergreen browse. Conifer and mixed stands with hemlock and balsam fir were very important wintering areas for moose, especially in the western portion of the study area. In central

Massachusetts, the lack of balsam fir increased reliance on high-density regenerating stands during winter. Additionally, mixed stands with hemlock and deciduous shrubs and saplings were also used heavily. Selection of vegetation that provided a combination of cover and access to abundant low-quality browse helped moose minimize their energy expenditure at a time when forage nutrition cannot meet body maintenance needs (Gasaway and Coady 1974, Peek 1997, Schwartz and Renecker 1997).

Vegetative cover types that supported winter browse such as conifers, mixed-conifer-hardwoods, and regenerating forest stands were used by moose until mid-April when the emergence of green vegetation marked the beginning of the growing season. Moose transitioned to foraging on more nutritious leafy deciduous vegetation as soon as it became available, as they attempted to maximize energy consumption (Belovsky 1978, Hjeljord et al 1990). Cover types that provided abundant deciduous vegetation, including deciduous forests, regenerating hardwood stands, mixed and deciduous wooded wetlands, and shrub wetlands, were heavily used during the growing season. Deciduous stands were used most intensively by males in central and western Massachusetts during spring. Males in western Massachusetts used greater amounts of deciduous forests than both males and females in central Massachusetts during spring and fall. Females did not show selection for deciduous forests in spring, likely because calving areas dominated female spring habitat use, and none of the females in this study used deciduous stands as calving sites. Wetlands that supported aquatic vegetation were also used throughout spring, summer, and fall. However, regenerating forests stands were the most heavily used cover type during the growing season.

Our analysis of core area use suggests that early successional regenerating forests created by logging appeared to be an important habitat type for moose in Massachusetts. Moose in central Massachusetts used areas of forest regeneration intensively in all seasons (43–68% of core area use and selection ratios ≥ 1.43 in all seasons). Use of regenerating stands by moose in western Massachusetts was more variable, but core area habitat use was still concentrated in these sites especially during summer, when the need to put on weight was greatest. Early seral stage forest stands provided a concentrated source of abundant browse during the growing season (McDonald et al. 2008), which allowed moose to maximize their forage intake without having to move over large areas to obtain it (Belovsky 1981, Wickstrom et al. 1984). The intense use of these sites ($\geq 56\%$ of home range core areas by all groups) during summer suggests that moose relied on regenerating forests to provide the browse they required to gain weight at this critical time of year. The high concentration of browse found in these sites mimicked permanent shrub communities, including delta floodplains, tundra and subalpine areas, and stream valley shrub communities, that are used heavily by moose in other portions of the range (Peek 1997), but are not present in southern New England.

The recent pattern of logging in Massachusetts appeared to be favorable to moose. About 60% of forest land in Massachusetts is controlled by non-industrial private forest owners in small-sized lots (mean = 4.8 ha) (Kittredge et al. 2003). Harvest sites on state and private lands were distributed randomly, with 1.5% of the forested landscape logged annually (Kittredge et al. 2003, McDonald et al. 2006), resulting in new patches of early successional habitat within a matrix of mature and maturing forest. The small size (16.5 ha) and moderate harvest intensity (27% of timber volume harvested) of forest harvest

units (Kittredge et al. 2003) resulted in short distance to edge, which provided direct access to both abundant browse and cover in close proximity to one another. Shelter cuts were commonly applied to harvest units and provided cover from solar radiation along with abundant 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 1997). Shelter cuts within hemlock and fir stands not only provided access to young deciduous browse, but also access to conifer browse during winter and cover year round.

The differences in seasonal use of vegetative cover types by moose in central and western Massachusetts may in part reflect the differences in the distribution and availability of forest cover in those areas of the state, as well as areas of adjacent Vermont and New Hampshire. Moose in western Massachusetts had greater amounts of deciduous forest available to them, but also showed seasonally higher selection ratios for deciduous forest stands than moose in central Massachusetts, indicating that the greater use was not merely the result of greater availability. Greater amounts of regenerating forest in the core areas of central area moose during winter may in part be due to a reduction or lack of this cover type in the home ranges of 2 moose that used portions of the Green Mountain National Forest in Vermont where no logging has occurred for 30 years. However, moose in areas of western Massachusetts with regenerating forest available to them also showed lower use compared to central Massachusetts moose.

Another factor that may have influenced selection of vegetative cover type by moose was the transition in forest types across the state. Differences in selection is at least partly caused by the different plant communities and stand structure in the 2

portions of the study area. Balsam fir occurred in the spruce-fir-northern hardwood forests at the highest elevations of western Massachusetts but was absent in central areas and lower elevation in western Massachusetts. In central Massachusetts the use of conifer and mixed-coniferous-deciduous stands increased in winter. However, with the absence of balsam fir, hemlock was the only conifer that made up a large portion of the winter diet of moose; white pine was avoided (Faison et al. 2010). Additionally, less restrictive snow conditions in central Massachusetts may have allowed for use of regenerating stands into late winter, while deep snow in western Massachusetts may have forced moose into the shelter of spruce-fir stands. Favored deciduous species, such as hobblebush (*Viburnum lantanoides*), striped maple, beech, and aspen were also less common in central Massachusetts compared to the spruce-fir-northern hardwood and northern hardwood-hemlock-white pine forests of western Massachusetts. While palatable forage was abundant in deciduous and mixed stands of the transitional hardwood and central hardwood-hemlock forests of central Massachusetts, the reduced amount of these key species seemed to limit use of this cover type in central Massachusetts compared to western areas. Despite this, deciduous stands made up twice the amount of spring core area use for central males than any other season, indicating selection for deciduous stands in spring compared to other seasons.

2.5.4 Movements

The annual pattern of movement rates can provide information on the timing of important ecological periods for moose. 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 1985, Cederlund 1989). In our

study, the reduced movement rates we observed during winter were typical of moose behavior throughout their range. Schwartz and Renecker (1997) discussed how lower metabolic rates, an adaptation to reduced forage abundance and quality during the dormant season, and increased time required for processing and ruminating food resulted in fewer daily feeding bouts and lower activity levels. Observed movement rates were further reduced during winter by periods of deep snow.

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).

Deviations in daily movement rate from the overriding influence of seasonal changes in vegetation were greatest at times of the year corresponding to the annual reproductive cycle of moose. At a time of year when movements would otherwise be at their peak, female daily movement rates were at their lowest level after giving birth to calves during the second week of May. Movement rates then slowly increased over the following month as calf mobility increased. In contrast, male movement rates were highest (2-3 times any other period) during the rut in late September and early October as they attempted to find and tend to potential mates.

Coady (1974) stated that increasing snow depths are correlated with more restrictive movements and suggested the following: at >40 cm movements begin to be slightly restricted; 60-70 cm, mobility is restricted; >70 cm, movements are impeded; and >90 cm, movements are greatly restricted and mortality can increase. Additionally, in

Massachusetts variable conditions of snowstorms produce conditions ranging from powder to heavy wet snow, to sleet and freezing rain. Repeated snowstorms combined with temperatures that fluctuate around freezing can lead to crusted and multilayered snow that can cause reduced mobility at depths less than those identified by Coady (1974). Accumulating snow depths in Massachusetts can be deep enough to inhibit movements by moose. Moose movement rates were extremely low during periods of deep and restrictive snow conditions, especially during February and March. However, snow depths and conditions can vary greatly year to year, and across the state. Higher elevations in western Massachusetts increased the likelihood of deep snow. When confined by deep snow moose concentrated their habitat use into as little as 22 ha for up to 6-10 weeks, others used areas of 50-60 ha for 6 weeks to 3.5 months. The variability in the timing, depth, and condition of snowfall strongly influenced the variability in early and late winter home range size, as moose moved widely between suitable winter habitats until confined by snow.

2.5.5 Temperature and Habitat Relationships

We speculate that periodically reduced rates in movements during spring, summer, and fall were the result of thermoregulatory behavior during periods of high temperature. Moose are potentially thermally stressed throughout the year in Massachusetts, but particularly so during spring through fall. Temperatures above 14° C result in increased metabolic rates (respiration and heart rate) in moose to reduce body temperature, while temperatures above 20° C cause moose to resort to open-mouthed panting (Renecker and Hudson 1986). Based on 7 years (2002 – 2008) of temperature data in central Massachusetts (Fig. 2.4) (Boose 2001), the mean maximum daily

temperature consistently exceeded the 14° C thermal stress level for summer from mid-April until mid-October, and exceeded the panting level for all of summer and for most of September. Mean daily minimum temperatures were above the 14° C threshold from late June until the last week of August, which corresponds to a dip in late summer movements by males in central and western Massachusetts.

The 14 and 20° C temperature thresholds suggested by Renecker and Hudson (1986) may be conservative for identifying thermal stress during spring and fall. These temperatures were derived for moose with their summer coat. During spring and fall moose either still retain their winter coats or have already grown it for fall. However, the Renecker and Hudson (1986) study was conducted with a small sample size ($n = 2$) of captive animals in Alberta, Canada. How well the identified thermal stress temperatures represent free-ranging animals on the southern edge of the species' range is unknown.

Moose select both wetlands and closed canopy forest as thermal cover when temperatures reach upper critical levels (Renecker and Hudson 1986, Schwab and Pitt 1991, Demarchi and Bunnell 1995, Dussault 2004). Wetlands, both wooded and other types, were used by moose from spring through fall, and provided important aquatic vegetation and relief from thermal stress. Closed canopy coniferous forests, mixed coniferous-deciduous forests, and deciduous forests were also used by moose as thermal shelters. Nocturnal use of open wetlands and regenerating sites and daytime use of wooded wetlands and closed canopy forests was common. Increased nocturnal activity during warm periods was previously reported for moose by Belovsky (1981) and Dussault et al. (2004), and for elk (Merrill 1991).

Moose were almost constantly subjected to thermal stress during summer. Large body size and low surface-area-to-volume ratios limit heat loss and made large males extremely susceptible to thermal stress. Mature males especially seemed to restrict their movements and home range size during summer and often occupied areas where regenerating stands with abundant browse were in close proximity to a wetland, making repeated movements back and forth throughout the season. Periods of high temperature that force moose into thermal refuges have the potential to limit the number and duration of foraging and feeding bouts at the time of year when weight gain is imperative (Belovsky 1981, Ackerman 1987, Demarchi and Bunnell 1995). These bouts, once missed, are difficult to compensate for due to constraints of the rumen cycle, which can have negative consequences for moose survival (Westoby 1974, Renecker and Hudson 1986, Iason et al. 1999).

2.5.6 Management Implications

The year-round intensive use of regenerating forests by moose in Massachusetts underlies the importance of early successional habitats for moose. The current pattern of logging that creates these habitats in a patchy mosaic on the landscape seems to be favorable for moose. However, recently adopted plans by the Massachusetts Department of Conservation and Recreation (DCR) to severely restrict and eliminate logging on some state forest lands and other DCR controlled properties could have a negative impact on moose. Moose rely on these high density forage sites, which mimic permanent shrub communities elsewhere in moose range, to gain weight for the winter and to support lactation of calves. Reduced disturbance through logging would remove this cover type from some of the largest conservation lands in the state, and from areas that make up a

large portion of suitable moose habitat. Loss of these habitats would force moose to forage for lower density browse in mature forest stands, which could result in higher energy expenditures to obtain the same amount of food. This could be particularly harmful for a species living in an environment at the extremes of its temperature tolerances, where minimizing energy expenditure to obtain food may be an essential survival strategy.

The emphasis on the importance of early successional habitats should not take away from that fact that moose require a mix of cover types and age classes to meet their annual habitat needs. Seasonally mature coniferous, mixed-coniferous-deciduous, and deciduous stands were used heavily by moose. Additionally, moose used mature forests and a variety of wetlands as thermal shelters during periods of high temperature, and mature coniferous and mixed-coniferous-deciduous stands during periods of deep snow. Management of moose habitat on a landscape scale in Massachusetts would ensure the protection of large blocks of forested habitat, which 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 habitat, and a variety of wetlands. This mix of vegetative cover types and age classes would provide suitable habitat not only for moose but for most wildlife species in the state.

Moose appear to be able to cope with the current levels of development on the uplands in most of central and western Massachusetts, but may be inhibited from using valley bottoms due to high human densities. Increasing urban sprawl in Massachusetts threatens moose and other wildlife by permanently converting natural habitats and further fragmenting what remains. Moose home range sizes can provide information to land

managers and conservationists on the space requirements of this wide ranging species, and demonstrate the importance of maintaining connectivity between large blocks of forested habitat for moose and other wildlife species.

The timing of increased movements in the spring and during the rut in the fall can help wildlife managers to inform the public of the increased likelihood of encountering moose crossing roadways and highways at these times of year, which also corresponds to annual peaks in moose vehicle collisions.

TABLES

Table 2.1 Habitat categories used to classify core area habitat use.

Classification	Included Habitats
Conifer	Coniferous forest and mixed coniferous dominated forest
Mixed	Mixed deciduous and coniferous forest
Deciduous	Deciduous forest and mixed deciduous dominated forest
Total Regeneration	Shelter regeneration, open regeneration and powerline right of way
Wooded Wetland	Conifer, mixed, and deciduous wooded wetlands
Wetland Other	Grassy fens, shrub swamps, bogs, deep wetlands, and open water
Developed	Human development
Open	Open fields

Table 2.2 Seasons used for calculating home-range, movements, and core-area analyses.

Season	Dates	Vegetation/Browse	Temperature ^a	Movement	Season length
Spring	16 April – 31 May	Growing season; bud-break-leaf out	Cool-Hot	Not snow restricted, potentially temperature restricted	45 Days
Calving (females)	8-13 May – 15 June	Growing season; bud-break-leaf out	Cool-Hot	Restricted by newborn calf	30 Days
Summer	1 June – 30 Aug	Growing season; full leaf out	Hot	Restricted by temperature	90 Days
Fall	1 Sept – 31 Oct	Leaf out to leaf off	Hot-Cool	Rut and temperature influenced	60 Days
Early Winter	1 Nov – 31 Dec	Dormant season; woody/evergreen	Warm-Cold	Not snow restricted, potentially metabolism restricted	60 Days
Late Winter	1 Jan – 15 April	Dormant season; woody/evergreen	Cold-Warm	Potentially snow and metabolism restricted	105 ys

^a Temperature ranges describing typical temperatures experience during a season; Cold $\leq 0^{\circ}\text{C}$, Cool $> 0^{\circ}\text{C}$ and $< 14^{\circ}\text{C}$, Warm $\geq 14^{\circ}\text{C}$ and $< 20^{\circ}\text{C}$, Hot $\geq 20^{\circ}\text{C}$.

Table 2.3 Collared moose identification, location, and collar performance.

Animal ID	Estimate Age	Sex	Location	Date	End of Data Acquisition	Number of Locations	Acquisition Rate	Animal Status June 30, 2011
<u>Central females</u>								
CF-1	Unknown ^a	FM	New Salem	19-Oct-06	5-Oct-07	3,023	80.2	Dead (broken leg)
CF-1		Recollar		5-Oct-07	7-Dec-07	617	93.3	
CF-2	Unknown	FM	Barre	19-Jan-07	18-Jan-08	3,130	80.6	Dead (capture)
CF-3	Unknown	FM	Pelham	7-Apr-07	30-Jan-08	1,668	82.3	Collar released
CF-3		Recollar		20-Feb-08	18-May-09	4,204	87.2	
CF-4	Unknown	FM	Prescott Peninsula	13-Oct-07	30-Apr-09	10,514	97	Collar released
CF-5	Unknown	FM	Petersham	22-Sep-08	30-Sep-09	3,581	89.7	Dead (MVC)
<u>Central males</u>								
CM-1	4-6	M	Royalston	1-Apr-06	31-Aug-06	893	55	Dead (NH hunt)
CM-1		Recollar		7-Dec-06	20-Oct-07	3,035	89.7	
CM-2	5-6	M	Hardwick	26-Sep-06	9-Sep-07	2,928	77.9	Collar Released
CM-2		Recollar		10-Sep-07	15-Jun-08	1,815	71.9	
CM-3	2-3	M	Prescott Peninsula	30-Sep-06	8-Sep-07	2,817	77	Collar Released
CM-3		Recollar		9-Sep-07	14-Jun-08	2,546	86.1	
CM-4	2-3	M	Pelham	24-Mar-07	22-Jul-07	904	79.2	Collar Released
CM-4		Recollar		17-Nov-07	21-Jan-09	3,766	83.2	

CM-5	4-5	M	Petersham	16-Oct-07	31-Dec-08	7,871	93.2	Collar Released
CM-6	5-6	M	Pelham	22-Oct-07	17-Sep-08	2,797	81.9	Collared
CM-6			Recollar	8-Dec-08	29-Jun-09	1,726	79.7	
CM-7	4-5	M	Montgomery	3-Oct-08	30-Apr-10	9,187	83.3	Collar Released
<u>Western males</u>								
WM-1	3-5	M	Florida	17-Sep-06	6-Jun-07	2,394	85.7	Dead (VT hunt)
WM-2	5-6	M	Washington	29-Sep-08	22-May-10	11,021	96	Dead (injury)
WM-3	1-2	M	Savoy	10-Sep-09	31-May-10	2,417	85.9	Collar Released
WM-4	3-5	M	Savoy	22-Sep-09	31-Aug-10	6,128	92.8	Collared
WM-4			Recollar	20-Oct-10	currently deployed			
WM-5	3-5	M	Huntington	26-Sep-09	10-Apr-10	3,712	85.7	Dead (Spring)
WM-6	2-3	M	Peru	11-Oct-09	15-Apr-11	10,412	98.4	Collar Released
WM-7	3-4	M	Peru	12-Oct-09	28-Feb-11	15,322	98.4	Collar Released

^a Exact age of females is unknown, but all females were mature and reproductively active.

Table 2.4. Seasonal and annual mean and median 100% minimum convex polygon home ranges (km²) for females in central Massachusetts and males in central and western Massachusetts.

<u>Central females</u>					<u>Central males</u>					<u>Western males</u>				
n	Mean	SE	Median	Range	n	Mean	SE	Median	Range	n	Mean	SE	Median	Range
7	30.3	7	27.9	14.1-70.1	14	30.1	4.3	28.5	12.9-61.8	7	50.5	18.3	36.4	18.6-158.1
6	39.2	10.9	31.2	18.2-92.3	9	24.1	4.7	20.3	7-48.5	5	26.2	5.6	28.2	6.2-37.3
5	23	3.1	27	12.8-28.8	8	41.4	8	37.3	6.6-84.8	6	214.9	89	114	39.3-546.8
6	23.8	3	23.9	14.9-33.9	11	31	7.1	22	9.7-85.3	10	44.3	8.9	38.3	14.6-103.6
7	28.6	3.8	27.4	15.5-43.7	12	25	5.7	19.6	8.4-80.4	7	19.2	4.8	18.8	5.1-39.1
6	64.9	9.4	60.6	41.6-103.2	8	73.3	12.9	58.2	33.5-133.6	6	164.5	62.6	103.6	56-458.9

Table 2.5. Seasonal and annual mean 95% fixed kernel density estimator home ranges (km²) for females in central Massachusetts and males in central and western Massachusetts ($h = 200$ m).

Season	<u>Central females</u>				<u>Central males</u>				<u>Western males</u>			
	n	Mean	SE	Range	n	Mean	SE	Range	n	Mean	SE	Range
Spring	6	10.9	1.3	7-15.6	13	15.6	1.3	9.2-27.9	7	19.3	3.11	12.7-32.7
Summer	6	17.3	3.8	8.7-34.8	9	13.5	1.7	6.3-22.5	5	14.6	3.9	5.2-21.4
Fall	5	12	0.9	10-15.3	7	18.7	2.2	6.5-23.1	5	29.8	5.6	18.7-44.8
Early Winter	6	11.9	1.4	8.4-15.9	11	13.2	1.9	4.6-26.6	10	12.6	0.9	9.8-18.1
Late Winter	7	13.3	0.8	11.6-17.9	12	9.9	1.9	4.7-26.2	7	7.4	1.3	4.1-12.4
Annual	5	26.7	2	19.9-32.1	7	25.4	4	20.2-51	5	35.2	5.1	22.6-45.4

Table 2.6. Scaled daily movement rates (m/day) for female moose in central Massachusetts and male moose in central and western Massachusetts.

Season	<u>Central females</u>				<u>Central males</u>				<u>Western males</u>			
	n	Mean	SE	Median	n	Mean	SE	Median	n	Mean	SE	Median
Spring	6	2402	157.4	1770	13	2330	120.8	1978	6	2234	331.9	1183
Calving	4	874	68.4	860	NA	NA	NA	NA	NA	NA	NA	NA
Summer	6	2509	242.8	2098	10	2153	288	1830	4	1649	140.5	1409
Fall	6	1846	97.2	1548	9	3451	353.6	2285	6	3464	381.4	2127
Early Winter	6	1544	123.5	1355	13	1881	161.5	1410	9	1543	121.8	1226
Late Winter	7	1298	193.9	1271	11	1310	110.6	1061	6	1064	102.1	871
Annual	5	1702	105.4	1398	6	2024	192.6	1542	3	1886	107.4	1287

Table 2.7. Unscaled daily movement rates (m/day) for female moose in central Massachusetts and male moose in central and western Massachusetts.

Season	<u>Central females</u>				<u>Central males</u>				<u>Western males</u>			
	n	Mean	SE	Median	n	Mean	SE	Median	n	Mean	SE	Median
Spring	6	2005	121.5	1454	13	2012	120.1	1739	6	2134	279.2	1833
Calving	4	670	113.8	579	NA	NA	NA	NA	NA	NA	NA	NA
Summer	6	2136	194.9	1800	10	1914	231.4	1657	4	1761	234.6	1512
Fall	6	1619	92.1	1336	9	3247	415.7	2121	6	3444	468.7	2104
Early Winter	6	1392	136.5	1127	13	1716	129.1	1321	9	1562	105.8	1253
Late Winter	7	1026	156.2	994	11	1154	98.6	919	6	1025	84	831
Annual	5	1468	104.5	1142	6	1939	104.5	1465	3	2041	196	1411

Table 2.8. Road densities for MCP and KDE home ranges (km/km²)

	<u>MCP outside KDE</u>		<u>MCP</u>		<u>KDE</u>	
	Mean	SE	Mean	SE	Mean	SE
Interstate Highways	0.00	0.00	0.00	0.00	0.00	0.00
Major State Highways	0.00	0.00	0.00	0.00	0.00	0.00
State Routes	0.13	0.03	0.11	0.03	0.06	0.01
Major Local Arteries	0.05	0.02	0.03	0.01	0.01	0.01
Local Paved Roads	0.40	0.05	0.30	0.08	0.14	0.09
Local Unpaved/Improved Forest Roads	0.54	0.06	0.49	0.13	0.44	0.03
Forest Roads	0.33	0.04	0.35	0.09	0.38	0.07

FIGURES

Figure 2.1. Study Area location in northeastern USA, depicted in blow-up with dashed line, located in west-central Massachusetts, USA and bordering areas of southern Vermont and New Hampshire. Darker colors represent higher elevation.

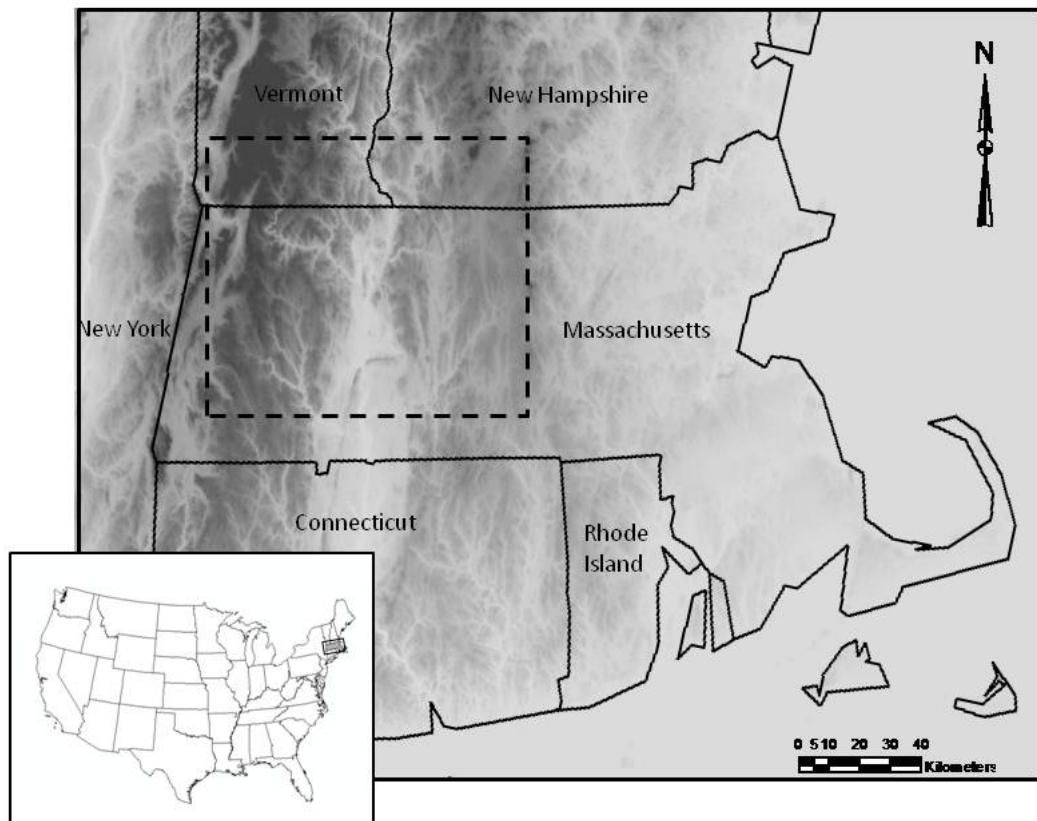


Figure 2.2. Species range of moose in the northeastern United States, states with moose populations shown in gray, approximate southern edge of species range depicted with dashed line, study area depicted with small insert rectangle.

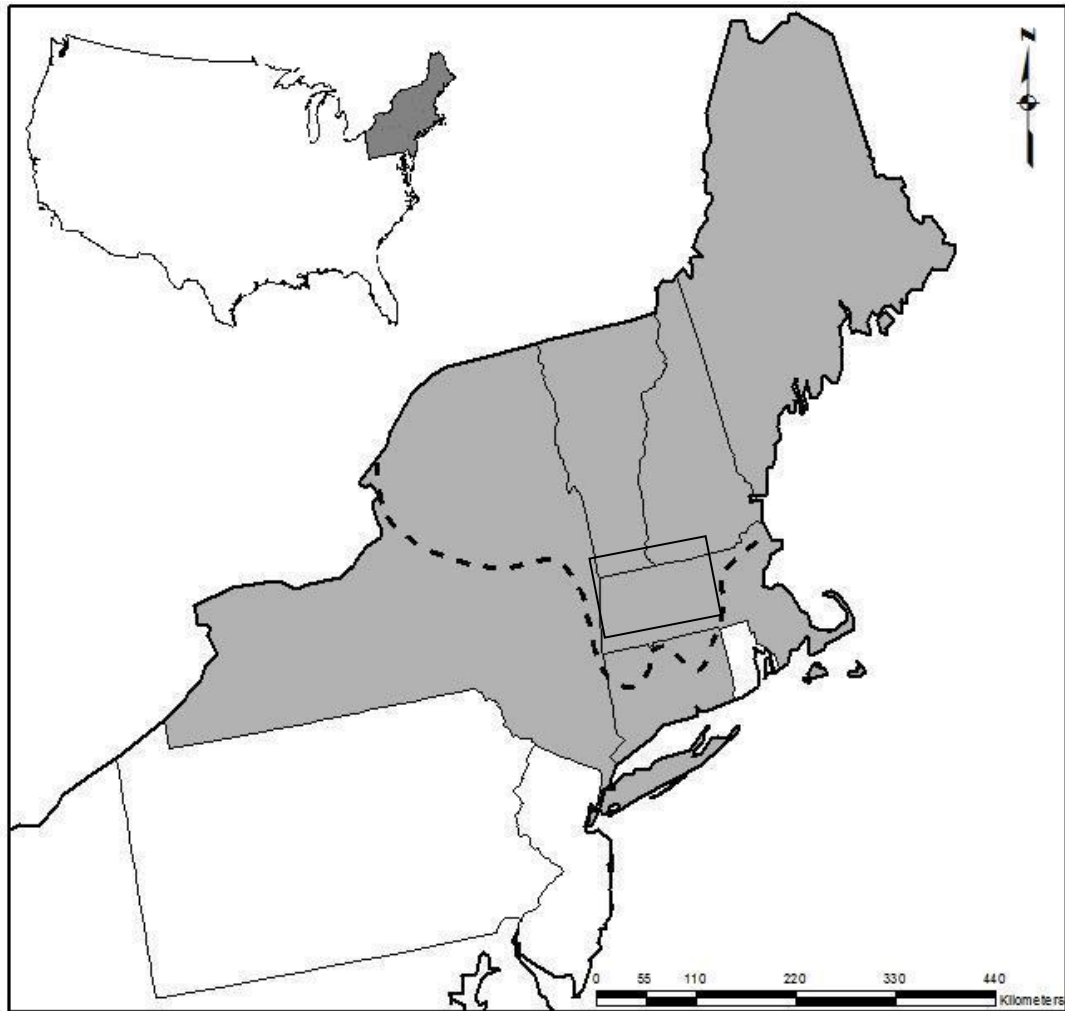


Figure 2.3. Forest Types of Massachusetts (after Westveldt et al. 1956 and DeGraaf and Yamasaki 2000), study area depicted with insert rectangle.

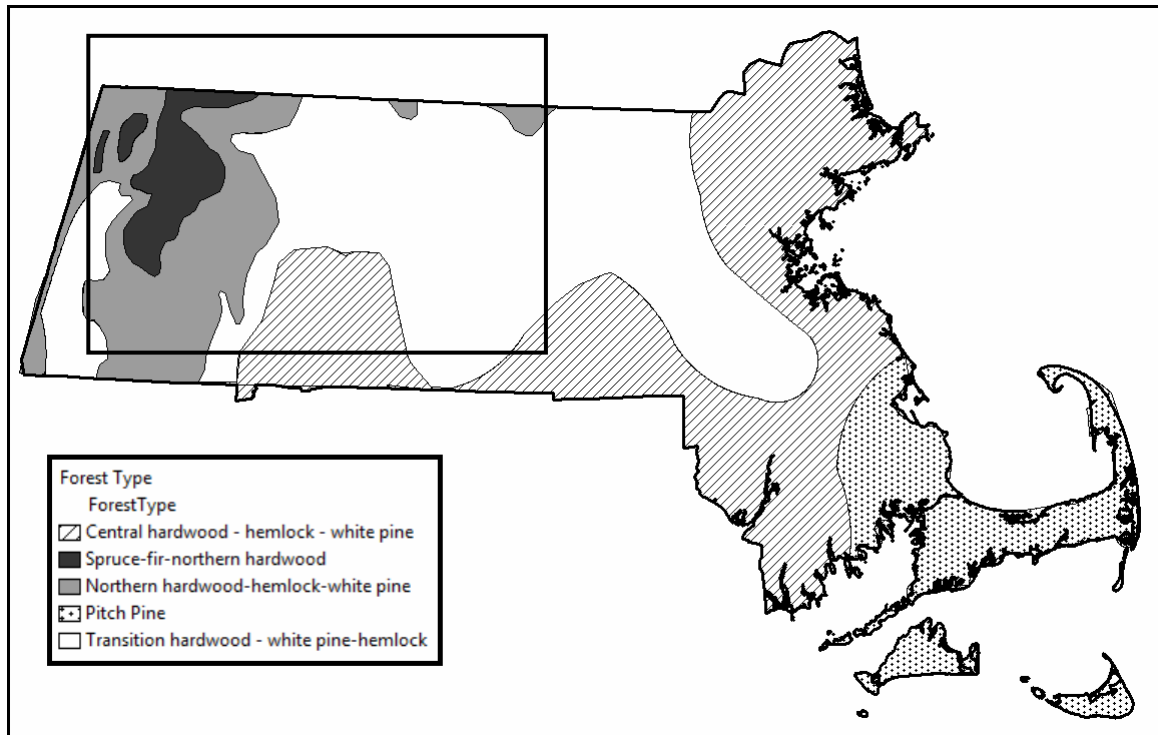


Figure 2.4. Comparison of mean daily maximum and minimum temperatures in central Massachusetts (Petersham, MA) to identified thermal stress temperatures that result in increased respiration in moose during summer (14°C) and winter (-5°C), top and bottom horizontal lines, respectively.

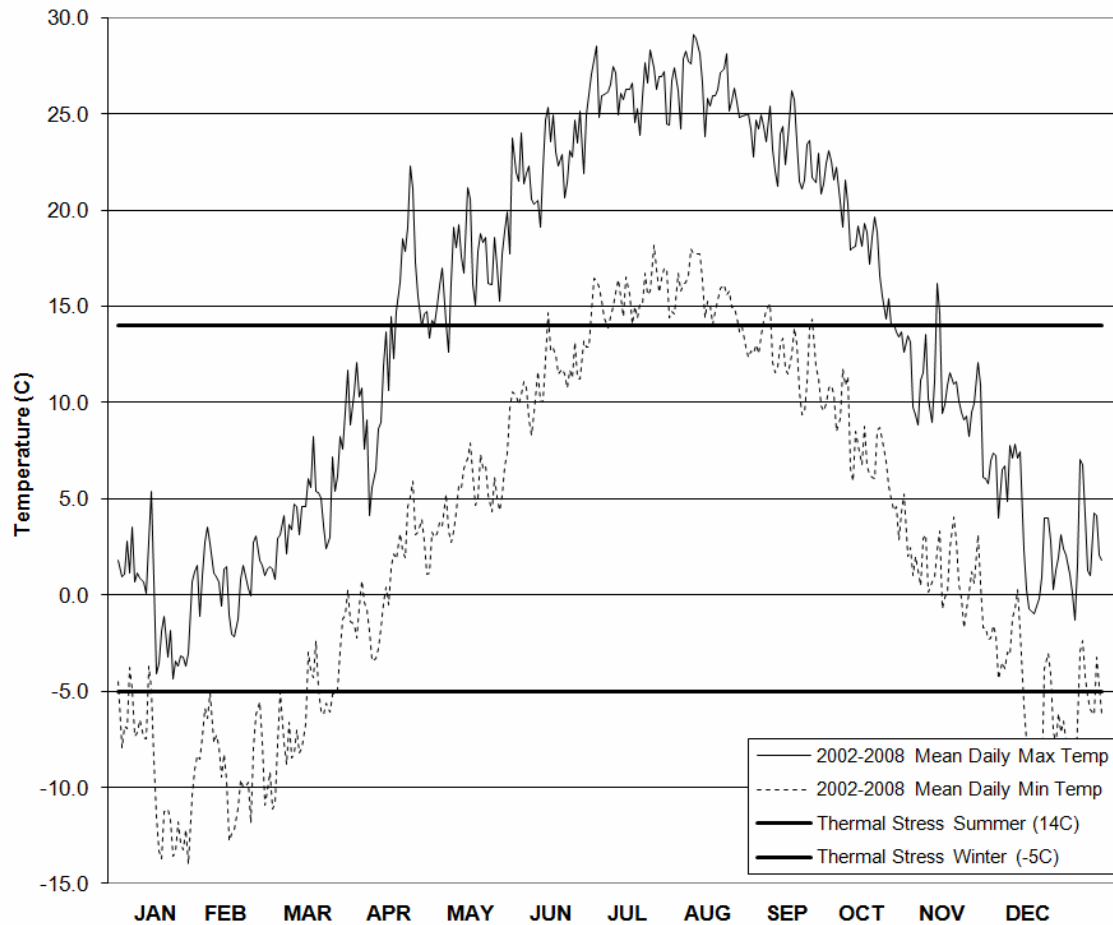


Figure 2.5. Five year modeled snow depth (cm) for representative towns in central (Royalston) and western (Savoy) Massachusetts.

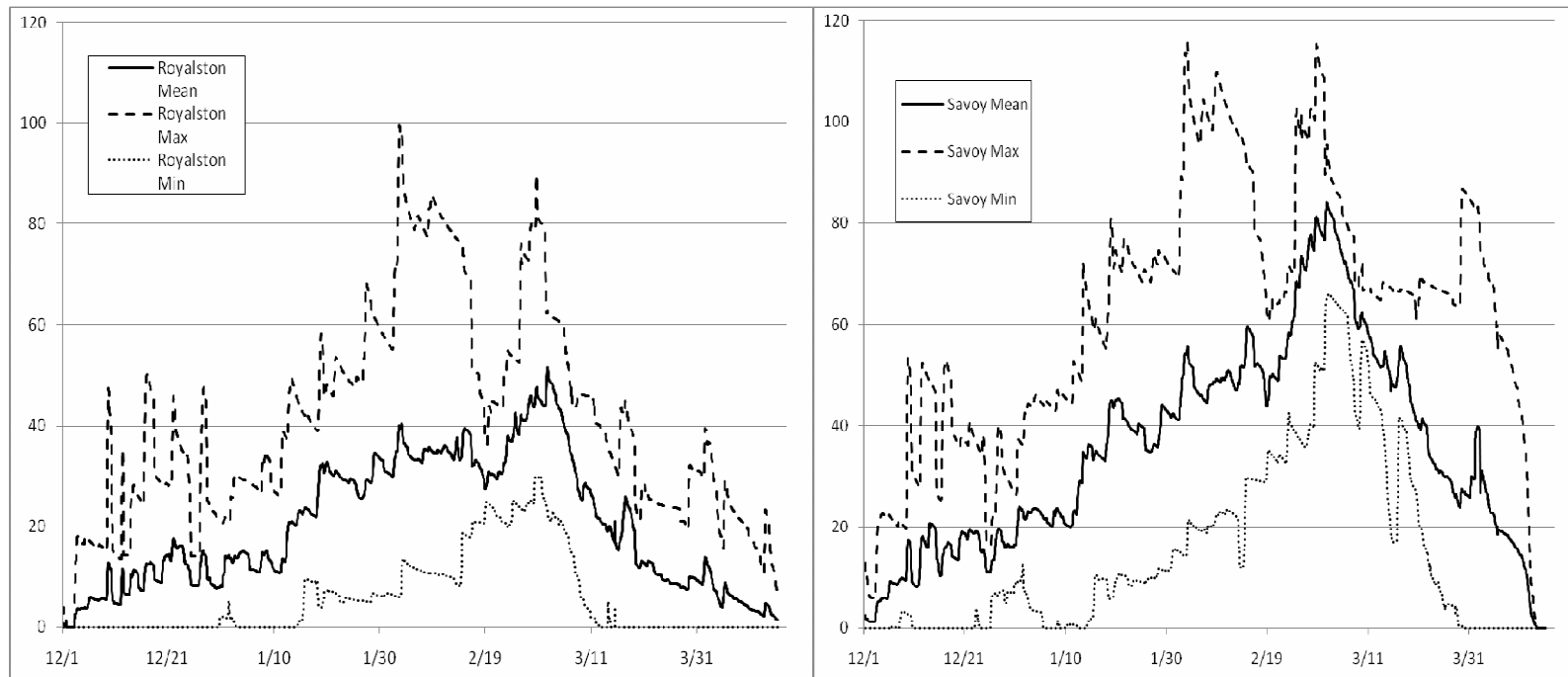


Figure 2.6. Mean daily movement rates (m/day) for female moose ($n = 5$) in central Massachusetts thin line, 10 day moving average to remove noise heavy line. Julian date on x-axis.

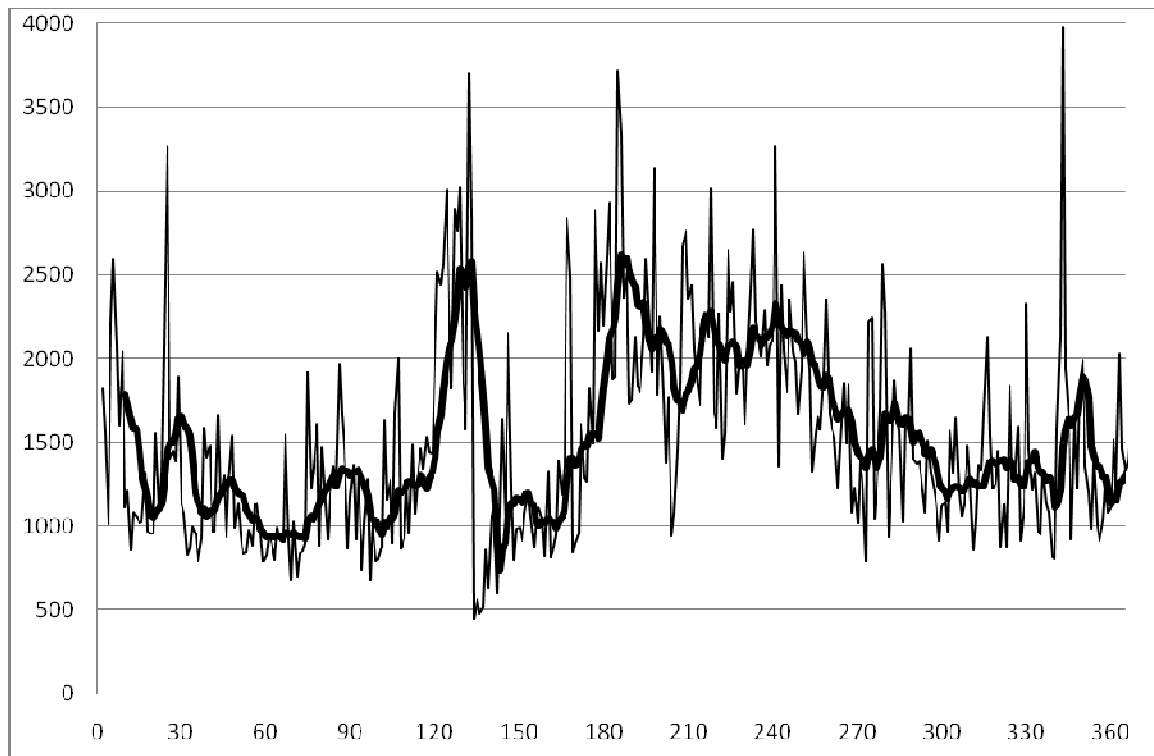


Figure 2.7. Mean daily movement rates (m/day) for male moose ($n = 7$) in central Massachusetts thin line, 10 day moving average to remove noise heavy line. Julian date on x-axis.

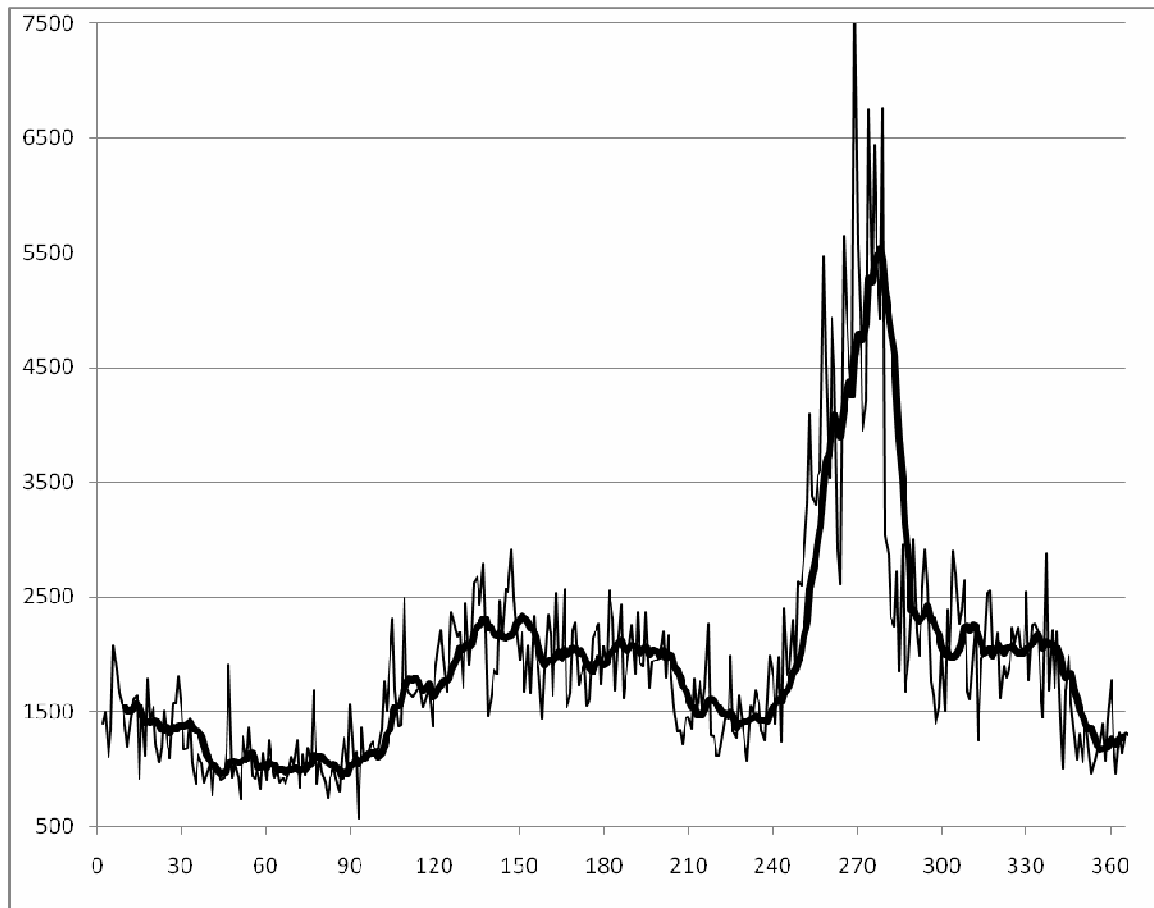


Figure 2.8. Mean daily movement rates (m/day) for male moose ($n = 7$) in western Massachusetts thin line, 10 day moving average to remove noise heavy line. Julian date on x-axis.

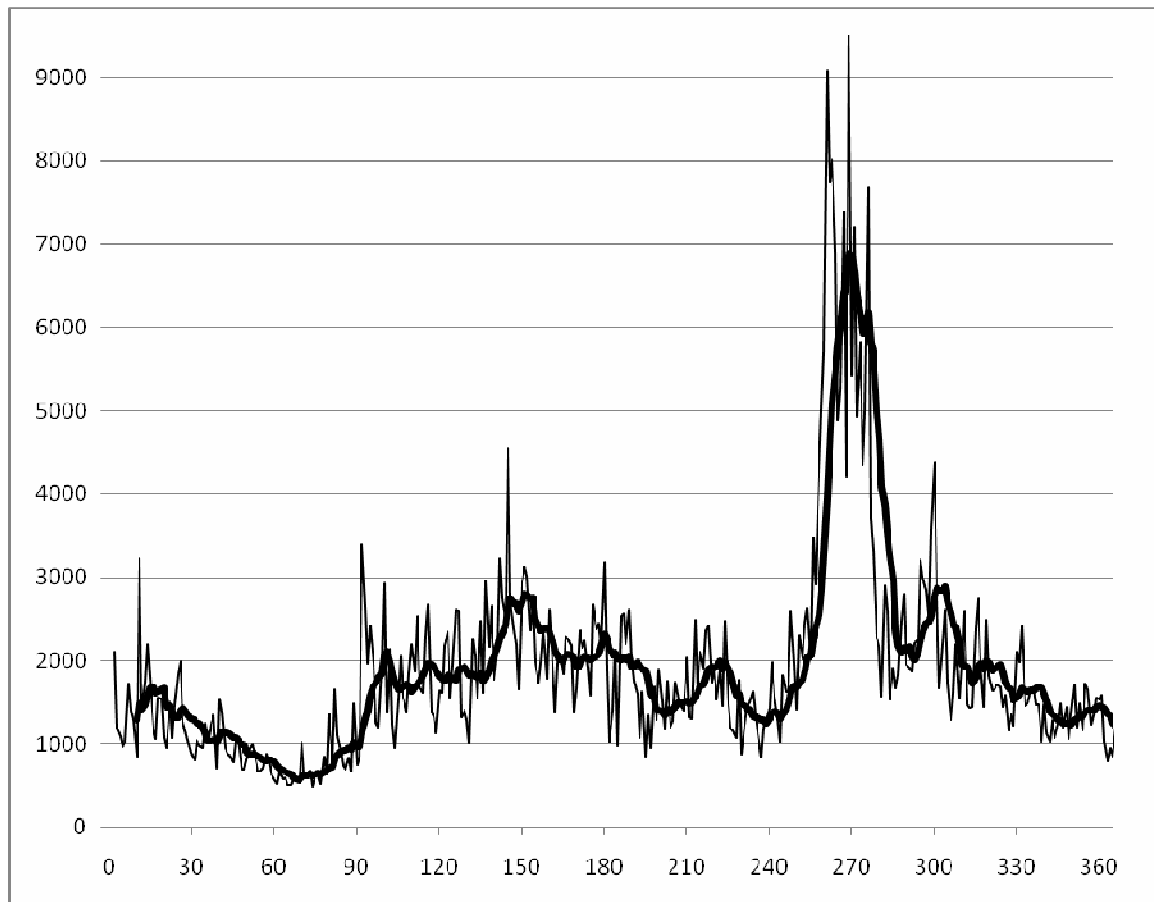


Figure 2.9. Proportion of available habitats in moose MCP home ranges, n = 5, 7, and 7 for Central females, Central males, and Western males, respectively.

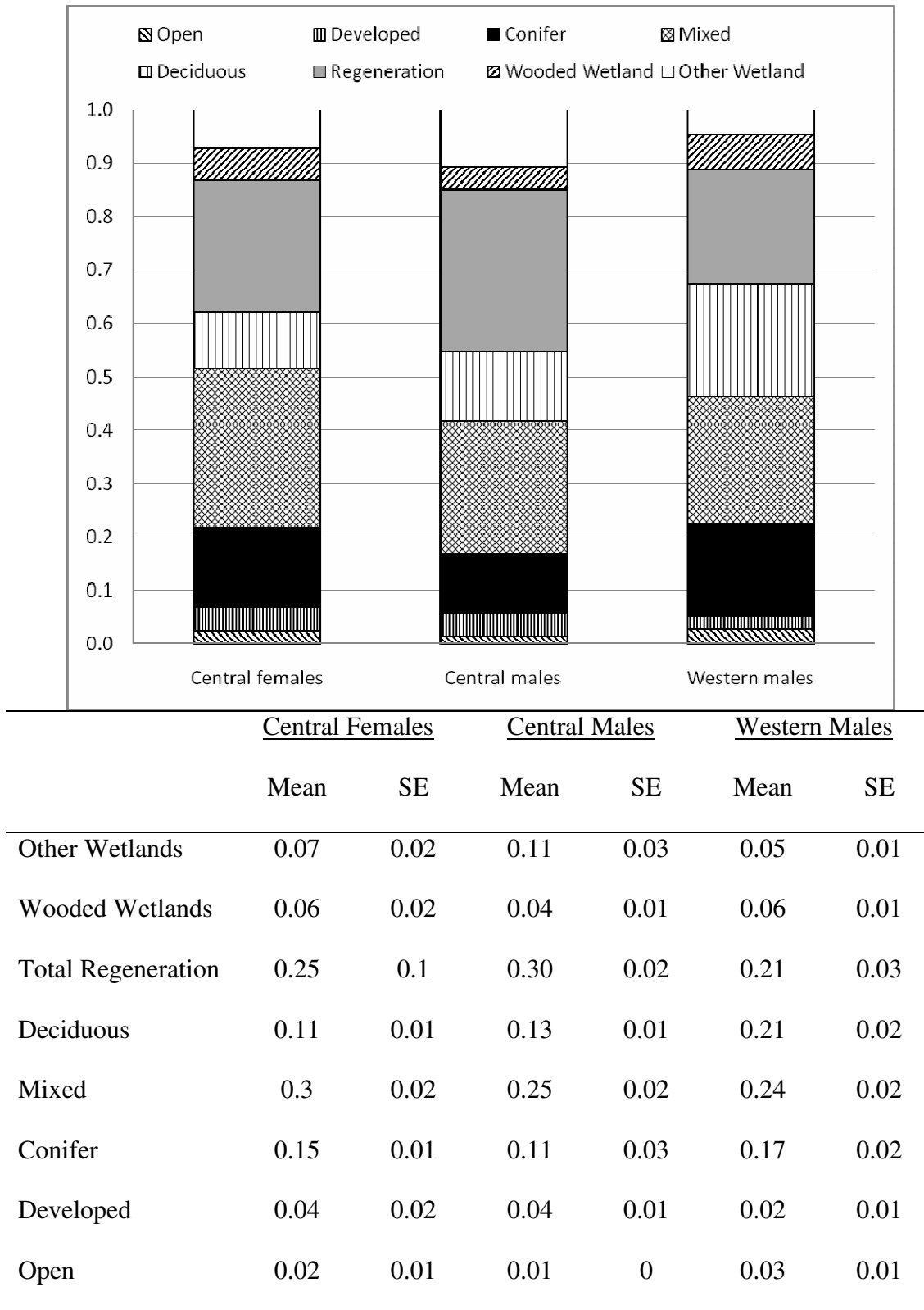


Figure 2.10. Seasonal proportional core area habitat use for female moose in central Massachusetts, n = 5, 5, 4, 5, and 5 for Spring, Summer, Fall, Early Winter, and Late Winter, respectively.

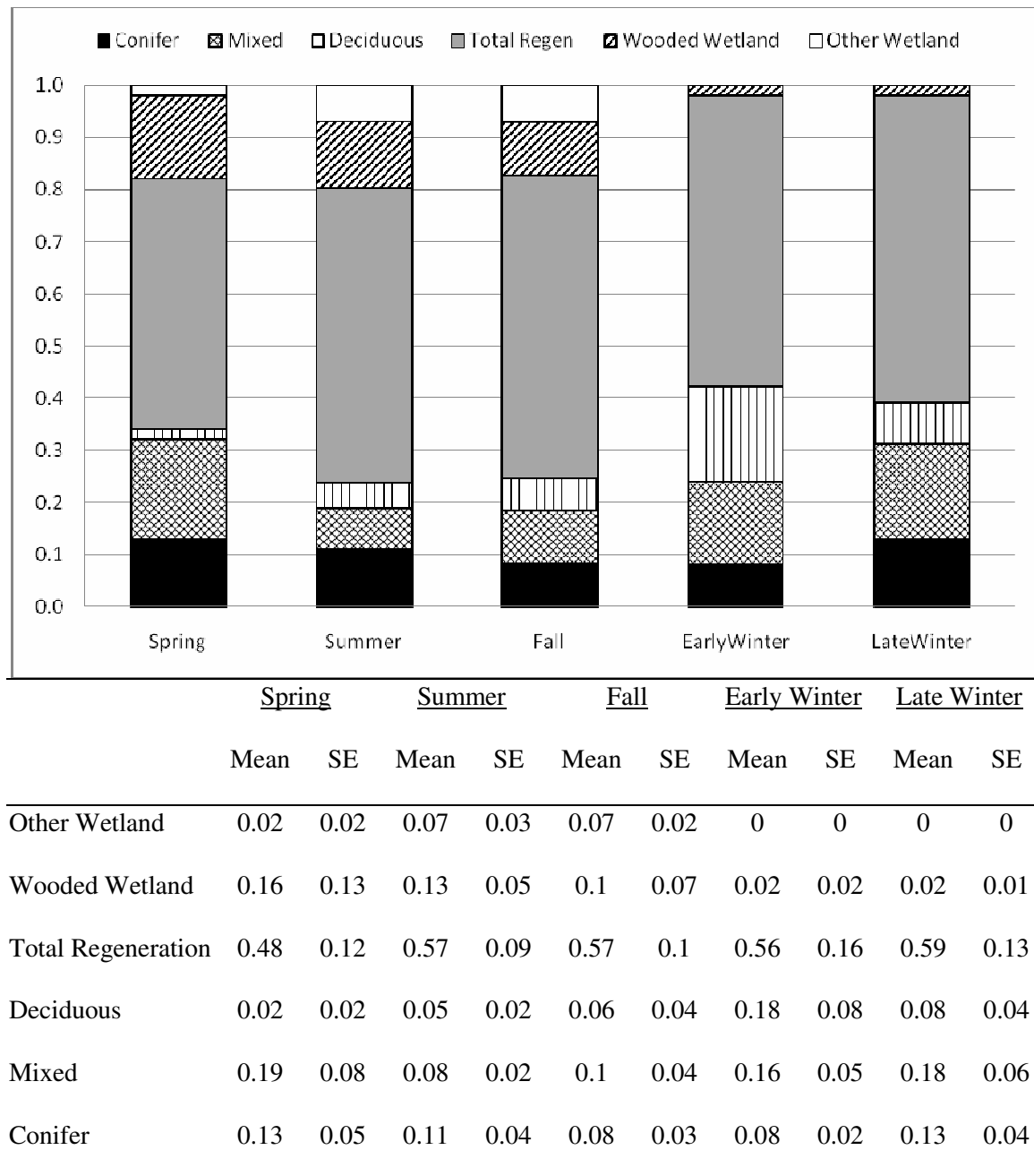
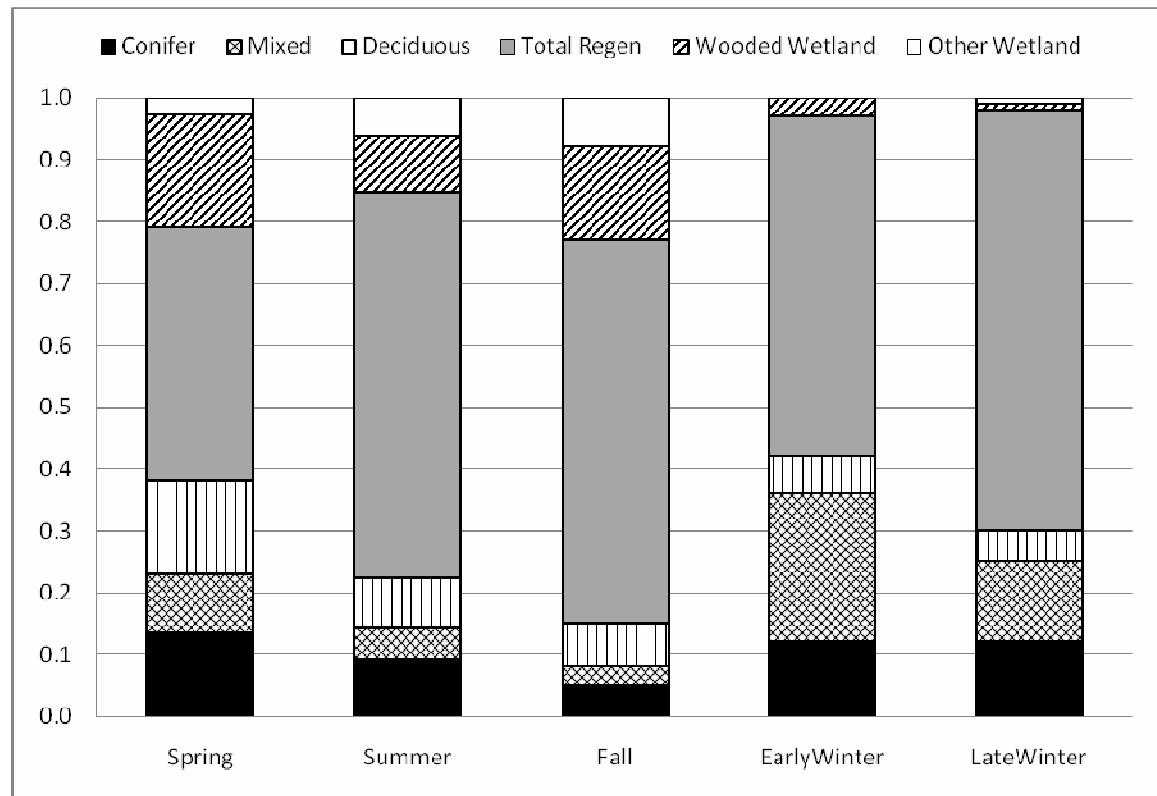
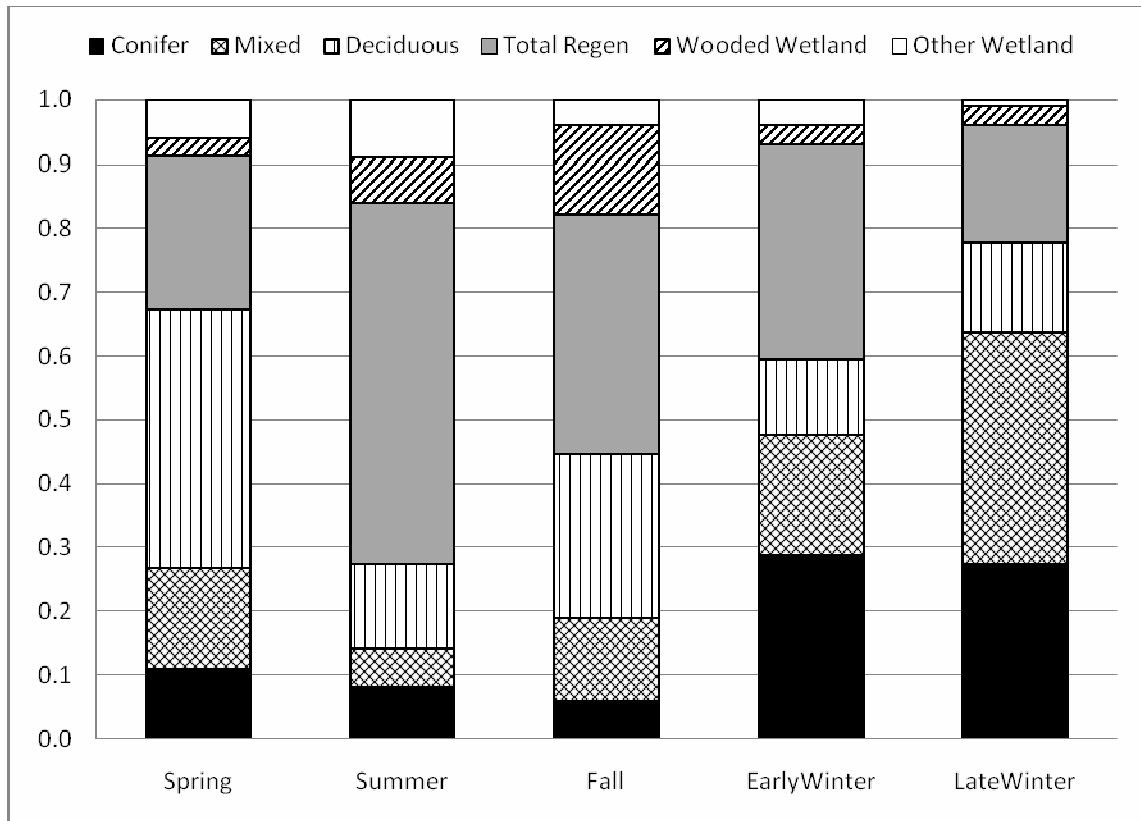


Figure 2.11. Seasonal proportional core area habitat use for male moose in central Massachusetts, n = 7, 7, 7, 6, and 7 for Spring, Summer, Fall, Early Winter, and Late Winter, respectively.



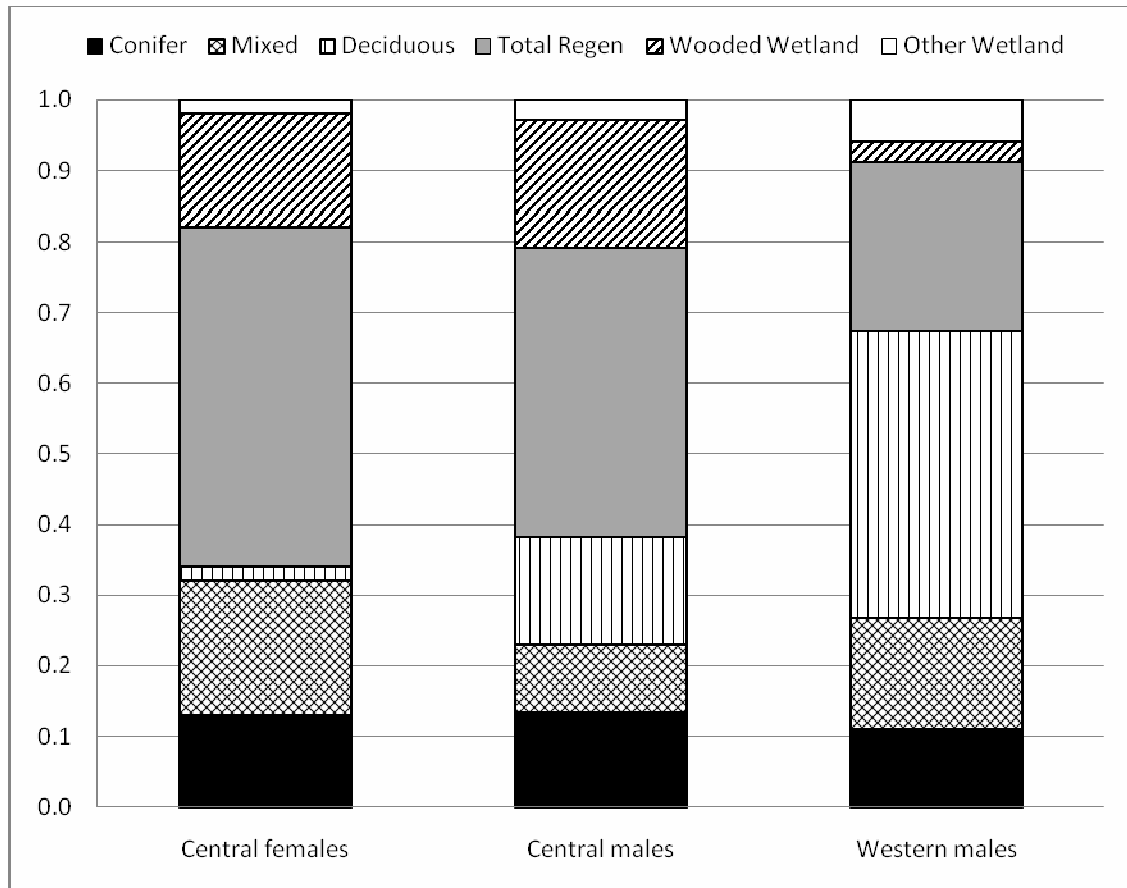
	<u>Spring</u>		<u>Summer</u>		<u>Fall</u>		<u>Early Winter</u>		<u>Late Winter</u>	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Other Wetland	0.03	0.01	0.06	0.02	0.08	0.03	0	0	0.01	0.01
Wooded Wetland	0.19	0.1	0.09	0.02	0.15	0.03	0.03	0.01	0.01	0
Total Regeneration	0.43	0.07	0.62	0.62	0.62	0.04	0.55	0.13	0.68	0.08
Deciduous	0.16	0.07	0.08	0.02	0.07	0.03	0.06	0.03	0.05	0.02
Mixed	0.1	0.03	0.05	0.02	0.03	0.02	0.24	0.1	0.13	0.05
Conifer	0.14	0.05	0.09	0.05	0.05	0.02	0.12	0.04	0.12	0.03

Figure 2.12. Seasonal proportional core area habitat use for male moose in western Massachusetts, n = 6, 5, 3, 7, and 6 for Spring, Summer, Fall, Early Winter, and Late Winter, respectively.



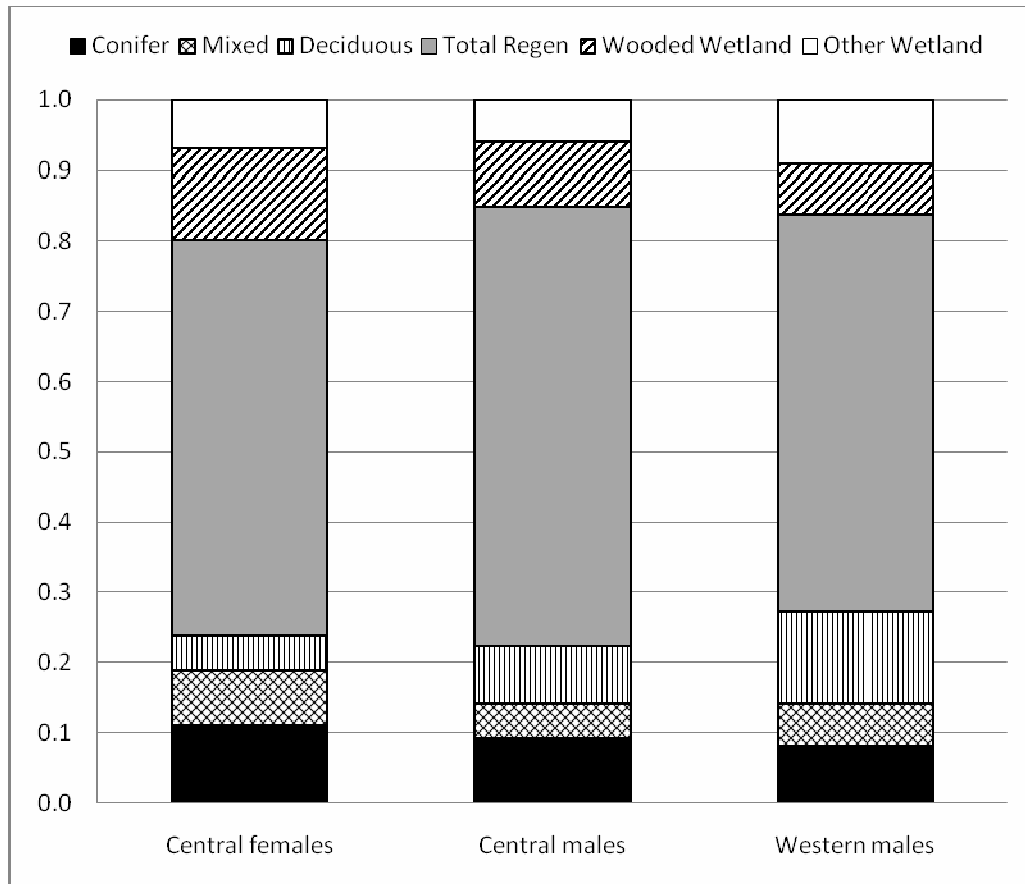
	<u>Spring</u>		<u>Summer</u>		<u>Fall</u>		<u>Early Winter</u>		<u>Late Winter</u>	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Other Wetland	0.06	0.01	0.09	0.07	0.04	0.02	0.04	0.02	0.01	0.01
Wooded Wetland	0.03	0.01	0.07	0.02	0.14	0.04	0.03	0.01	0.03	0.02
Total Regeneration	0.24	0.08	0.56	0.04	0.38	0.14	0.34	0.09	0.18	0.05
Deciduous	0.41	0.07	0.13	0.06	0.26	0.07	0.12	0.05	0.14	0.09
Mixed	0.16	0.06	0.06	0.02	0.13	0.08	1.9	0.05	0.36	0.07
Conifer	0.11	0.02	0.08	0.03	0.6	0.02	0.29	0.05	0.27	0.06

Figure 2.13. Spring proportional core area habitat use for moose in central and western Massachusetts, n = 5, 7, and 6 for Central females, Central males, and Western males, respectively.



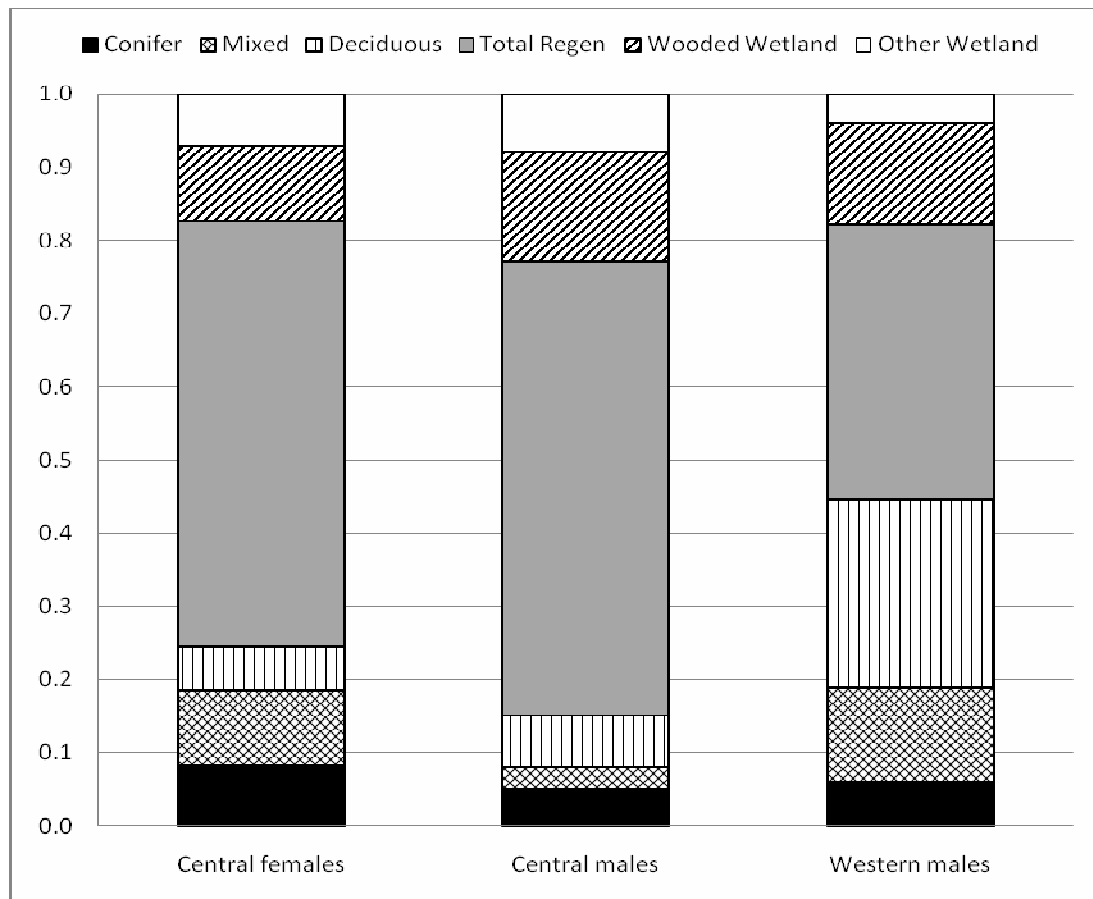
	<u>Central Females</u>		<u>Central Males</u>		<u>Western Males</u>	
	Mean	SE	Mean	SE	Mean	SE
Other Wetland	0.02	0.02	0.03	0.01	0.06	0.01
Wooded Wetland	0.16	0.13	0.19	0.1	0.03	0.01
Total Regeneration	0.48	0.12	0.43	0.07	0.24	0.08
Deciduous	0.02	0.02	0.16	0.07	0.41	0.07
Mixed	0.19	0.08	0.1	0.03	0.16	0.06
Conifer	0.13	0.05	0.14	0.05	0.11	0.02

Figure 2.14. Summer proportional core area habitat use for moose in central and western Massachusetts, n = 5, 7, and 5 for Central females, Central males, and Western males, respectively.



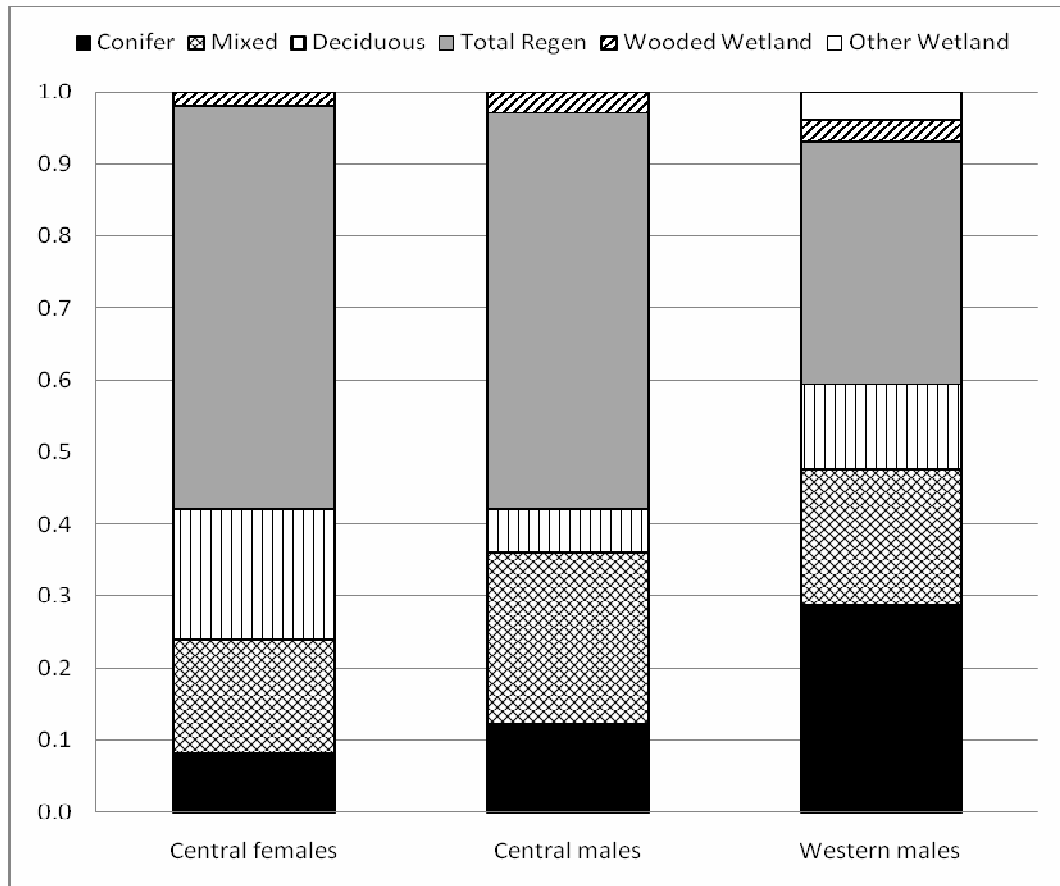
	<u>Central Females</u>		<u>Central Males</u>		<u>Western Males</u>	
	Mean	SE	Mean	SE	Mean	SE
Other Wetland	0.07	0.03	0.06	0.02	0.09	0.07
Wooded Wetland	0.13	0.05	0.09	0.02	0.07	0.02
Total Regeneration	0.57	0.09	0.62	0.62	0.56	0.04
Deciduous	0.05	0.02	0.08	0.02	0.13	0.06
Mixed	0.08	0.02	0.05	0.02	0.06	0.02
Conifer	0.11	0.04	0.09	0.05	0.08	0.03

Figure 2.15. Fall proportional core area habitat use for moose in central and western Massachusetts, n = 4, 7, and 3 for Central females, Central males, and Western males, respectively.



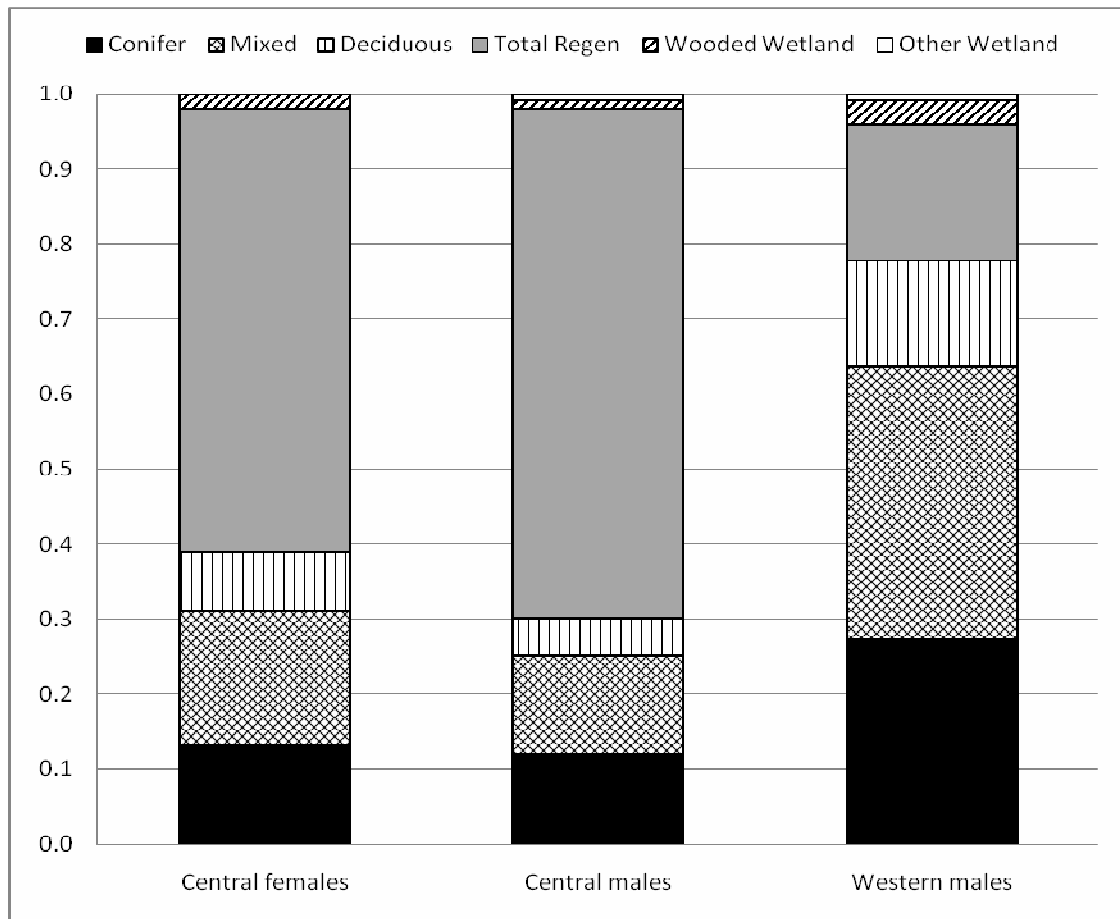
	<u>Central Females</u>		<u>Central Males</u>		<u>Western Males</u>	
	Mean	SE	Mean	SE	Mean	SE
Other Wetland	0.07	0.02	0.08	0.03	0.04	0.02
Wooded Wetland	0.1	0.07	0.15	0.03	0.14	0.04
Total Regeneration	0.57	0.1	0.62	0.04	0.38	0.14
Deciduous	0.06	0.04	0.07	0.03	0.26	0.07
Mixed	0.1	0.04	0.03	0.02	0.13	0.08
Conifer	0.08	0.03	0.05	0.02	0.6	0.02

Figure 2.16. Early winter proportional core area habitat use for moose in central and western Massachusetts, n = 5, 6, and 7 for Central females, Central males, and Western males, respectively.



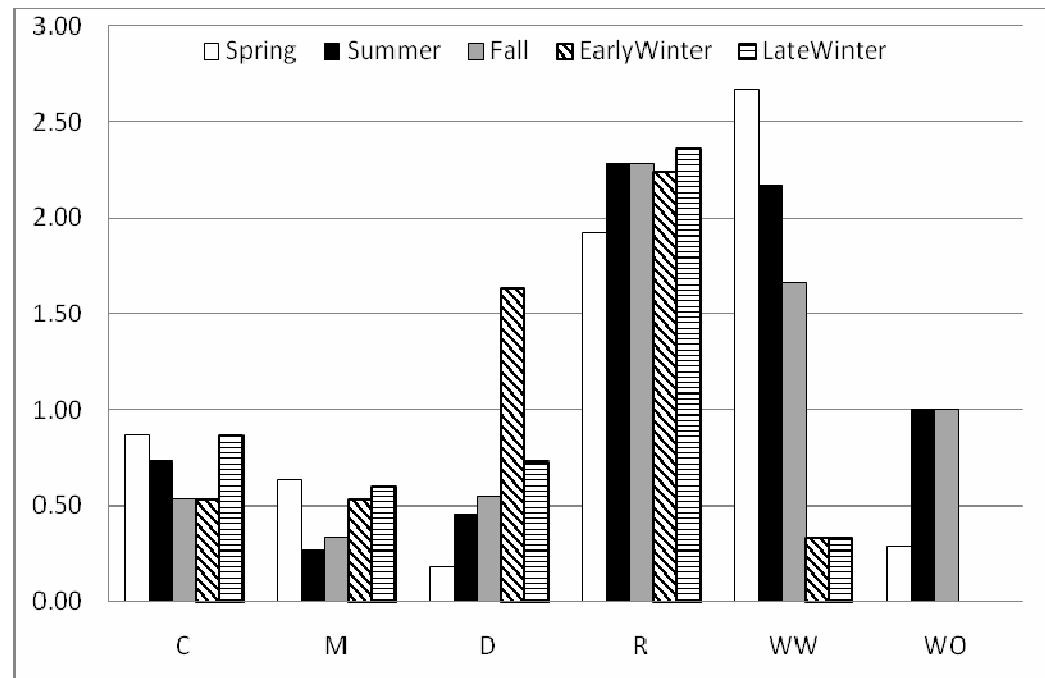
	<u>Central Females</u>		<u>Central Males</u>		<u>Western Males</u>	
	Mean	SE	Mean	SE	Mean	SE
Other Wetland	0	0	0	0	0.04	0.02
Wooded Wetland	0.02	0.02	0.03	0.01	0.03	0.01
Total Regeneration	0.56	0.16	0.55	0.13	0.34	0.09
Deciduous	0.18	0.08	0.06	0.03	0.12	0.05
Mixed	0.16	0.05	0.24	0.1	1.9	0.05
Conifer	0.08	0.02	0.12	0.04	0.29	0.05

Figure 2.17. Late winter proportional core area habitat use for moose in central and western Massachusetts, n = 5, 7, and 6 for Central females, Central males, and Western males, respectively.



	<u>Central Females</u>		<u>Central Males</u>		<u>Western Males</u>	
	Mean	SE	Mean	SE	Mean	SE
Other Wetland	0	0	0.01	0.01	0.01	0.01
Wooded Wetland	0.02	0.01	0.01	0	0.03	0.02
Total Regeneration	0.59	0.13	0.68	0.08	0.18	0.05
Deciduous	0.08	0.04	0.05	0.02	0.14	0.09
Mixed	0.18	0.06	0.13	0.05	0.36	0.07
Conifer	0.13	0.04	0.12	0.03	0.27	0.06

Figure 2.18. Seasonal use-availability ratios for female moose in central Massachusetts, n=5, 5, 4, 5, and 5 for Spring, Summer, Fall, Early Winter, and Late Winter, respectively.



	<u>Conifer</u>		<u>Mixed</u>		<u>Deciduous</u>		<u>Total Regeneration</u>		<u>Wooded Wetland</u>		<u>Open Wetland</u>	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Spring	0.86	0.31	0.63	0.27	0.2	0.18	1.92	0.48	2.7	2.12	0.25	0.25
Summer	0.7	0.25	0.26	0.06	0.42	0.2	2.28	0.37	2.13	0.78	1.03	0.47
Fall	0.52	0.18	0.32	0.13	0.55	0.32	2.26	0.41	1.72	1.16	1.02	0.34
Early Winter	0.52	0.16	0.52	0.18	1.65	0.71	2.23	0.65	0.38	0.25	0	0
Later Winter	0.85	0.25	0.6	0.19	0.75	0.33	2.35	0.5	0.34	0.5	0.05	0.05

Figure 2.19. Seasonal use-availability ratios for male moose in central Massachusetts, n = 7, 7, 6, 7, and 7 for Spring, Summer, Fall, Early Winter, and Late Winter, respectively.

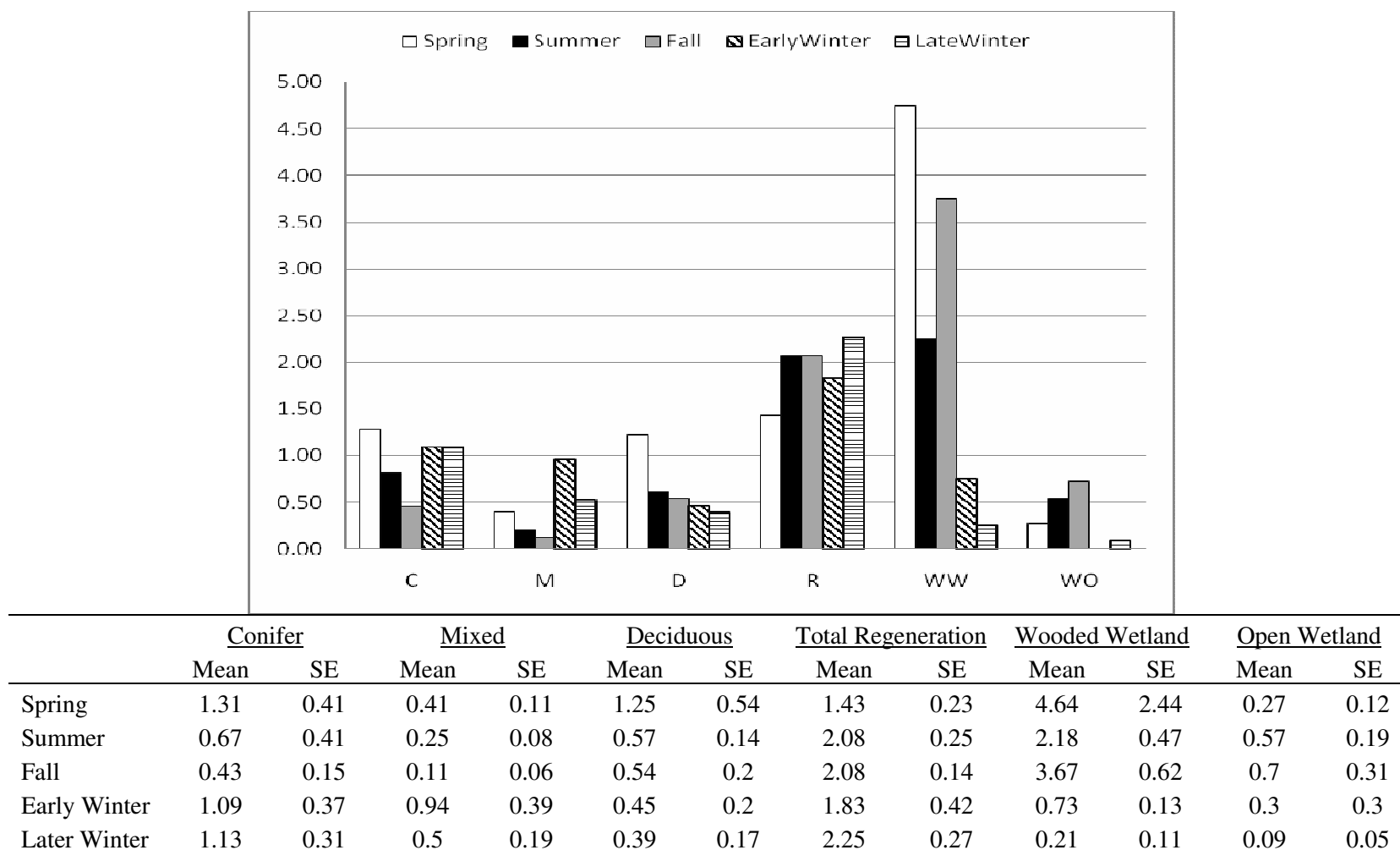
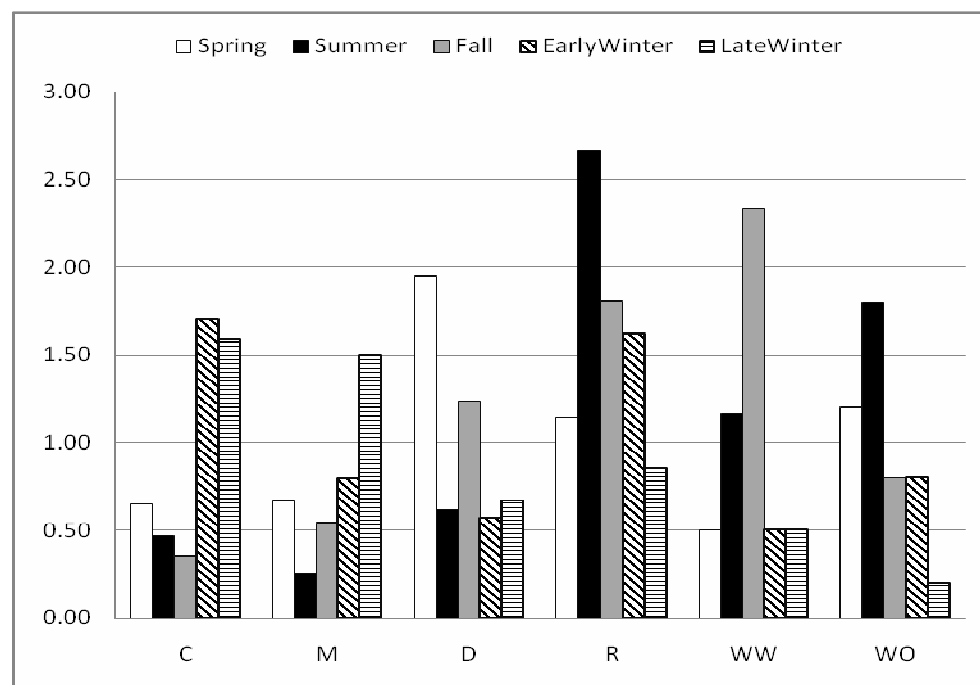


Figure 2.20. Seasonal use-availability ratios for male moose in western Massachusetts, n = 6, 5, 3, 7, and 6 for Spring, Summer, Fall, Early Winter, and Late Winter, respectively.



	<u>Conifer</u>		<u>Mixed</u>		<u>Deciduous</u>		<u>Total Regeneration</u>		<u>Wooded Wetland</u>		<u>Open Wetland</u>	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Spring	0.62	0.14	0.66	0.23	1.96	0.34	1.12	0.36	0.99	0.21	0.58	0.22
Summer	0.38	0.2	0.57	0.28	0.87	0.58	2.08	0.67	1.13	0.5	1.82	1.55
Fall	0.32	0.11	0.56	0.33	1.24	0.31	1.82	0.68	2.38	0.7	0.85	0.37
Early Winter	1.69	0.31	0.77	0.19	0.56	0.23	1.62	0.43	0.45	0.19	0.84	0.48
Later Winter	1.56	0.32	1.48	0.28	0.65	0.43	0.86	0.24	0.45	0.28	0.23	0.23

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