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The effect of thermoregulation and roads on the movements and habitat selection of moose in Massachusetts

David W. Wattles
University of Massachusetts - Amherst

THE EFFECT OF THERMOREGULATION AND ROADS ON THE MOVEMENTS AND HABITAT SELECTION OF MOOSE IN MASSACHUSETTS

A Dissertation Presented

by

DAVID WILLIAM WATTLES

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Approved as to style and content by:

_____
Stephen DeStefano, Chair

_____
Todd K. Fuller, Member

_____
Thomas Millette, Member

_____
Curtice R. Griffin, Department Head
Department of Environmental Conservation

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ABSTRACT

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MOVEMENTS AND HABITAT SELECTION OF MOOSE IN
MASSACHUSETTS**

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DAVID WILLIAM WATTLES, B.S., LAFAYETTE COLLEGE

M.S., UNIVERSITY OF MASSACHUSETTS AMHERST

Ph.D., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Stephen DeStefano

Massachusetts, U.S.A. is located along the southern boundary of the geographic

range of moose (*Alces alces*) in North America. This is an atypical environment for

moose, because of its extremely high levels of human development and high year-round

temperatures, which are possibly at the limits of moose physiological tolerances. I

investigated the role of these two factors on moose movements and habitat selection to

determine how human development of the landscape and temperature influence moose

occupation of this extreme environment. In addition, the response of moose to these

factors provides insights into the influence of development and temperature on individual

fitness and population persistence.

Thermal conditions in Massachusetts were consistently higher than the reported

physiological tolerances of moose, and higher than parts of the range where high

temperatures have negatively affected moose reproduction and survival. Moose greatly

reduced their selection of open foraging habitat and increased selection for thermal

shelters as temperatures increased above upper critical limits; this same pattern was

apparent when comparing day (warmer) to night (cooler) activities. A strong transition in

the use of habitats occurred at dawn and dusk, which corresponded to peaks in hourly movement rates at these times, indicating a transition in state from foraging at night to bedding during the day. The ability of moose to adapt to this extreme thermal environment through thermoregulatory behaviors reveals the limitations of predicting species distributions based solely on theoretical temperature tolerances.

Massachusetts has one of the highest rates of moose-vehicle collisions (MVCs) per-capita moose and resulting human fatalities. The majority (86%) of MVCs occurred on roads with high speed limits and traffic volumes, and occurred on these roads at much higher rates than would be predicted based on their availability on the landscape. The dense road network in Massachusetts had a strong negative effect on the movements and habitat selection patterns of moose. Moose avoided crossing roads and greatly reduced their use near roads. Road avoidance increased with increasing disturbance intensity associated with higher traffic volumes and busier times of day. Roadways reduced habitat availability and connectivity, were a major source of additive mortality for moose.

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CHAPTER 1

THERMOREGULATORY BEHAVIOR OF MOOSE: A NORTHERN UNGLULATE AT THE SOUTHERN EDGE OF ITS GEOGRAPHIC RANGE

1.1 Abstract

Moose (*Alces alces*) are well adapted to cold northern environments; however, they can experience hyperthermia at relatively low temperatures. Established upper critical temperatures for moose are between -5 and 0°C in winter and between 14 and 20°C in summer, and high temperatures are thought to be the main factor limiting the southern extent of their geographic distribution. Massachusetts, U.S.A. is located along the southern boundary of the geographic range of moose in North America. I assessed the thermal environment in Massachusetts and evaluated its suitability for moose. I then analyzed movement rates, activity patterns, and habitat use and selection relative to ambient temperature and time of day of collared moose to determine if moose were responding behaviorally to the thermal environment. Thermal conditions in Massachusetts were consistently higher than the reported physiological tolerances of moose, and were higher than in parts of the range where high temperatures have negatively affected moose reproduction and survival. Moose greatly reduced their selection of open foraging habitat and increased selection for thermal shelters as temperatures increased above upper critical limits; this same pattern was apparent when comparing day (warmer) to night (cooler) activities. A strong transition in the use of habitats occurred at dawn and dusk, which corresponded to peaks in hourly movement rates at these times, indicating a transition in state from foraging at night to bedding during the day. The magnitude of the reduction in use of open foraging habitat and increase in use of thermal cover relative to high temperatures was greater than has been reported for other portions of moose range where temperature-habitat use interactions have been studied.

Climate change and increasing temperatures could potentially cause a northward shift of the geographic range of moose. However, the ability of moose to adapt to this extreme thermal environment through thermoregulatory behaviors reveals the limitations of predicting species distributions based solely on theoretical temperature tolerances. Other factors, including the presence or absence of predators or parasites, or habitat quality and configuration, along with thermal stress, will likely influence moose population dynamics and determine if and where localized population declines occur.

1.2 Introduction

Climate and local weather play a major role in influencing the distribution of flora and fauna (Gaston 2003). The range of temperatures that a species can tolerate, and that allow it to survive and reproduce, are one of the factors that control where organisms are found. These temperatures can be used to define the species' thermal envelope, and this is one method used to delineate a species' range (Pearson and Dawson 2003 and references therein). As a result, the prospect of global climate change has raised questions about the persistence and future distributions of many wildlife species. Several studies have observed and predicted northward range shifts for many plant and animal species and communities (Parmesan and Yohe 2003, Parmesan 2006).

Moen (1968:1041) defined the thermal neutral range of homeotherms as "the heat exchange conditions which do not elicit a metabolic response to maintain normal body temperatures". Temperatures within this range, also known as the thermal neutral zone, can be delineated with lower and upper critical temperatures (LCT and UCT, respectively). By definition, conditions outside this range require an individual to expend excess energy to maintain normal body temperatures. Several factors can influence the thermal environment of an

animal and either raise or lower operative temperature (the temperature experienced by an animal) relative to ambient temperature, including solar radiation, wind, and water (Moen and Jacobsen 1974, Moen 1968, Moen 1982, Parker and Gillingham 1990, Mysterud and Ostbye 1999). Exposure to intense solar radiation can raise operative temperature of an animal or environment considerably, whereas convective cooling from wind and air circulation or conductive cooling from exposure to water can reduce the operative temperature.

Animals can respond physiologically or behaviorally to cope with operative temperatures outside their thermal neutral zone. Individuals can alter their behavior to take advantage of various conditions in their environment in order to reach or move closer to a thermal neutral state, thereby expending less energy for metabolic cooling. Animals can change their daily activity patterns by reducing movement and overall activity, or become more nocturnal and crepuscular, thereby limiting exposure to solar radiation and the heat of the day. They can also reduce exposure to radiation by taking advantage of landscape features or vegetation that provide cover. Topography and vegetation can both influence exposure to the cooling effects of wind, and the use of water and wetlands can help in conductive cooling. However, these actions may contribute to an overall negative energy state if they result in decreased food intake, which can ultimately lead to reduced body condition, greater susceptibility to parasites, disease, and predators, and reduced survival (Murray et al. 2006; Lenarz et al. 2009, 2010).

Moose (*Alces alces*) are strongly associated with the boreal forest of high northern latitudes and are well adapted for life in cold environments. Large body size, low surface-area-to-volume ratio, and a dark, dense insulating coat help to minimize heat loss and protect them from the cold. However, these adaptations may be a hindrance during warm periods and in warmer climates. Moose begin to experience hyperthermia at relatively low ambient

temperatures. Based on experiments with captive moose (Renecker and Hudson 1986, McCann et al. 2013), exponential increases in heart rate, respiration, and metabolic rates occurred in moose at temperatures above -5° C in winter and 14° C in summer, respectively, while temperatures above 0° C in winter and 20° C in summer caused open mouthed panting. Ackerman (1987) also noted consistent increased respiratory rates in wild moose at operative temperatures above 30° C on Isle Royale, Michigan. Renecker and Hudson (1986) reported that metabolic rate increased at a rate of 0.7 kJ/hour/kg BW-0.75/^{o} C and heart rate increased at a rate of 0.9 beats/minute/^{o} C at temperatures above the seasonal UCTs. Additionally, respiratory rates increased at a rate of 3.2 breaths/minute/^{o} C at temperatures above the seasonal UCT, to >40 breaths/minute at temperatures over 11° C in winter and over 60 breaths/minutes at temperatures over 20° C in summer.

Warm temperatures and thermal stress have been considered one of the most important -- if not the most important -- factor limiting the southern extent of moose distribution (Kelsal and Telfer 1974, Renecker and Hudson 1986, Peek and Morris 1998, Karns 1997). Telfer (1984) noted that the southern distribution of the species in North America closely matches the 20° C isotherm for July. Additionally, there is increasing agreement from across their range that moose are performing thermoregulatory behaviors to adapt to conditions outside their thermal neutral zone (Schwabb and Pitt 1991, Dussault et al. 2004, Borders et al. 2012, van Beest et al. 2012, Melin et al. 2014; however see also Lowe et al. 2010, Mech and Fieberg 2014).

Recently, moose numbers have been in decline in several places along the southern edge of the range in North America, including Minnesota (Murray et al. 2006; Lenarz et al. 2009, 2010), New Hampshire, Nova Scotia (Broders et al. 2012), Montana (DeCesare et al. 2014), and Wyoming. In Minnesota, where the decline has been most severe, high temperatures and global

warming have been thought to be interacting with parasites and disease in driving that decline (Murray et al. 2006; Lezarz et al. 2009, 2010; however see Mech and Fieberg 2014). At the same time, however, moose have expanded the extent of their range to the south in the northeastern United States (Wattles and DeStefano 2011). These seemingly conflicting events raise the question of how moose appear to be in severe decline in one portion of their southern geographic range yet are able to the south and become established in another.

The objectives of this study were to assess the thermal environment along the southern edge of the moose's geographic range in the northeastern United States and evaluate its suitability for occupation by moose. We documented how frequently temperatures in central Massachusetts exceeded the upper critical temperatures of moose, compared the thermal environment in Massachusetts to that in northeast Minnesota (where Lenarz et al. [2009] determined high temperatures were affecting moose survival), and determined if thermal shelters (vegetation cover that would allow moose to find relief from ambient conditions outside their thermal neutral zone) were available in the landscape that moose could use to limit their exposure to heat stress. Ultimately, we wanted to determine how moose were responding to the thermal environment of southern New England, if they were altering their habitat use and activity patterns to cope with high temperatures, and what were the potential consequences of those behaviors.

1.3 Study Area

The study area was located in the southern extent of moose range in northeastern North America, in central and western Massachusetts and adjacent portions of Vermont and New Hampshire (between 42° 9' and 42° 53' N latitude and 71° 53' and 73° 22' W longitude) (Fig. 1). Topography is dominated by glaciated hills with abundant small stream valleys, lakes, ponds,

and palustrine wetlands whose size and nature varies with changes in beaver (*Castor canadensis*) activity. The central and western sections of the study area are separated by the Connecticut River Valley, which runs N-S through west-central Massachusetts. Elevation ranges from 100 m above sea level in the Connecticut River Valley, to 425 m in the hills of central Massachusetts, to 850 m in the Berkshire Hills of western Massachusetts.

The western two-thirds of Massachusetts was >80% mixed deciduous, second- or multiple-growth forest, much of it resulting from regeneration of farm fields abandoned in the mid-to-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 hardwoods, northern hardwoods-eastern hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*), transition hardwoods-white pine-hemlock, and central hardwoods-hemlock-white pine. Dominant species included spruce (*Picea* spp.), balsam fir (*Abies balsamea*), American beech (*Fagus grandifolia*), birch (*Betula* spp.), trembling aspen (*Populus tremuloides*), eastern hemlock, oaks (*Quercus* spp.), hickories (*Carya* spp.), and maples (*Acer* spp.), depending on area and type (see DeGraaf and Yamasaki [2001] and Wattles and DeStefano [2013a] for a more detailed description of forest types). Transitions between forest types can be gradual or distinct depending on localized physiography, climate, bedrock, topography, land-use history, and soil conditions, resulting in a patchwork of forest types and species groups (Westveldt et al. 1956, DeGraaf and Yamasaki 2001).

Early successional habitat was created primarily through timber harvesting, and occasionally through wind and other weather events. During 1984-2000, about 1.5% of the forest was harvested annually, consisting of small (mean = 16.5 ha) cuts of moderate intensity (removal of 27% of timber volume) widely distributed on the landscape (Kittredge et al. 2003, McDonald

et al. 2006). The pattern of forest harvest and transitional forest types, as well as a history of

glaciation, provided a patchy mosaic of well-interspersed forest types, age classes, and wetlands.

Massachusetts is a coastal state and has a maritime climate. July was the warmest month,

when mean high temperatures ranged between 26-29° C, and January the coldest when mean

high temperatures ranged between 0 to -2° C (Fig. 2). Mean annual precipitation was 119 cm in

central areas and 124 cm in western areas, with all months receiving 8-12 cm (The Weather

Channel 2011a, 2011b).

1.4 Methods

1.4.1 Assessing the Thermal Environment

1.4.1.1 Seasons

We *a priori* defined the length and timing of 5 seasons based on several ecological

factors such as vegetation phenology (leaf out, leaf drop, dormancy), weather (including

temperature and snow conditions), and the moose reproductive cycle (Table 1). The 5 seasons

included spring, summer, fall, and early and late winter. To facilitate comparison of a heat stress

index (HSI) between Massachusetts and Minnesota, and for that analysis only, we used the

seasons identified by Lenarz et al. (2009): Late Spring (April and May), Warm Season (April

through October), January, and Cold Season (November through March).

1.4.1.2 Ambient Temperatures versus Upper Critical Temperatures (UCTs)

We calculated the mean number of days per season that the daily minimum, mean, and

maximum temperatures exceeded the upper critical temperatures for moose, as originally

estimated by Renecker and Hudson (1986), as 14° C and 20° C in summer and -5° C and 0° C in

winter; the lower temperatures invoked exponential increases in respiratory rate, heart rate, and

metabolic rate and the upper temperatures caused thermal panting. The critical cut-offs for summer were confirmed by McCann et al. (2013). Identifying the appropriate UCT for spring and fall was more difficult, as moose are shedding or growing their winter coats and likely experience thermal stress at temperatures between the summer UCT and winter UCT. We therefore present spring and fall temperatures relative to both summer and winter thresholds.

We obtained temperature data during 2002-2008 from the Fisher Meteorological Station at Harvard Forest, Petersham, Massachusetts (42.53311 N, 72.18968 W, 342 m elevation), which was located centrally in our study area (Fig. 1). Temperature was recorded by a Vaisala HMP45C Temperature and Relative Humidity Probe, positioned 2.2m above ground (Boose 2001). Temperature data were not available for the western portion of our study area for 2002-2008. We therefore compared temperatures relative to seasonal UCTs and calculated a HSI for this period only for the central study area.

1.4.1.3 Heat Stress Index (HSI)

The comparison of ambient temperatures and UCTs revealed how frequently temperatures exceeded the UCT each season; however, it did not quantify the magnitude by which each UCT was exceeded. To do this, we calculated a heat stress index (HSI) for Massachusetts after the method of Lenarz et al. (2009), who compared ambient temperatures recorded at a weather station established in their study area in northeast Minnesota to the UCT for moose. This involved comparing the daily minimum and maximum temperatures to the UCT and summing the differences across a season. We performed similar calculations, using the formula:

$$\sum_{t=day_1}^{day_i} \text{HSI} = (t_{min} - \text{UCT}_{metabolic})$$

Where HSI = Heat Stress Index for the season, t_{min} = the minimum ambient temperature for day i, and $UCT_{metabolic}$ = the Upper Critical Temperature where moose experience metabolic and other physiological responses to temperature. This was repeated for the maximum daily temperature (t_{max}) and the Upper Critical Temperature where moose experience panting ($UCT_{panting}$) for each season, resulting in 4 HSI values for each season. On days where the minimum or maximum temperature did not exceed the UCT, we added zero to the HSI value. For comparison purposes, we calculated the HSI for the same years (2002-2008) and seasons as Lenarz et al. (2009).

1.4.1.4 Thermal Shelters

To measure temperatures in potential thermal shelters in the study area, we placed Thermochron i-button temperature sensors (Embedded Data Systems, Lawrenceburg, Kentucky, USA) in 8 blocks of closely associated stands of regenerating forest, mature hemlock, and mature deciduous trees. We selected blocks where the 3 stand types were found in close proximity (<1 km), to insure that any temperature differences detected were due to stand type and not localized differences in climate. We placed two temperature sensors in each stand type in each block. Within stands, locations were selected that were out of direct sunlight, 50-100 m apart, and a minimum of 50 m from the edge of the stand. We placed the temperature sensors in pockets made from fiberglass window screening that we stapled to the north side of a 1 m tall wooden survey stake. We programmed the sensors to record a temperature reading every 60 minutes from August of 2008 until August of 2009.

1.4.2 Moose Habitat Use and Thermoregulatory Behavior

1.4.2.1 Capture and Marking

We captured adult (>1 yr old) moose by opportunistically stalking and darting them from the ground between March 2006 and November 2009. Moose were immobilized using either 5 ml of 300 mg/ml or 3 ml of 450 mg/ml xylazine hydrochloride (Congaree Veterinary Pharmacy, Cayce, South Carolina, USA) administered from a 3 or 5 cc Type C Pneudart dart (Pneudart, Inc., Williamport, Pennsylvania, USA). We used Tolazolene (100 mg/ml) at a dosage of 1.0 mg/kg as an antagonist. Moose were fitted with GPS collars, either ATS G2000 series (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) or Telonics TWG-3790 GPS collars (Telonics, Inc., Mesa, Arizona, USA). We programmed the collars to attempt a GPS fix as frequently as possible while allowing the battery life to extend for at least 1 year; depending on the collar, a GPS fix was attempted every 135, 75, or 45 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 at a preprogrammed date. Capture and handling procedures were approved by the University of Massachusetts Institutional Animal Care and Use Committee, protocol numbers 25-02-15, 28-02-16, and 211-02-01.

1.4.2.2 Temperature-Habitat Interactions

We used ArcGIS 9.3 (Environmental Systems Research Institute, Inc. 2008) to map GPS location data from collared moose. We mapped the data on 1:5000 Color Ortho Imagery collected in 2004-2005 and again in 2008-2009, available through the Massachusetts Office of Geographic Information (MassGIS 2011), 2003 and 2009 National Agricultural Imagery Program (NAIP 2011) satellite imagery, and mid-1990s black and white orthophotographs (VCGI 2011). We used Massachusetts Department of Environmental Protection wetlands

polygon and arc layers to identify wetlands (MassGIS 2011), as well as state wetland layers for Vermont (VCGI 2011) and New Hampshire (NH GRANIT 2011). Because the available GIS landuse layers did not accurately identify forest structure and composition (e.g., deciduous versus coniferous growth and age classes), we manually delineated and identified forest types and age classes. We identified early successional patches visually using the ortho-imagery and a statewide layer of forest harvest plans (McDonald et al. 2006). We manually classified each GPS location into 1 of 8 habitat classes: coniferous forest (mostly coniferous with minimal deciduous component), deciduous forest (mostly deciduous with minimal coniferous component), mixed forest (mixed deciduous and coniferous), regenerating forest (logged areas <20 years old and powerline right-of-ways), wooded wetlands (conifer, mixed, and deciduous wooded wetlands), other wetlands (grassy fens, shrub swamps, bogs, deep wetlands, and open water), open (e.g., fields and meadows), and developed. We set the age restriction of regenerating forest at 20 years because while logged areas >20 years old may still provide browse, these stands more closely resemble mature forest stands in quantity of browse and thermal properties. In addition, older harvests were difficult to distinguish and map accurately.

We merged ambient temperature data with GPS collar locations to represent ambient temperature conditions experienced by moose. We obtained temperature data from weather stations located centrally in either portion of the study area (Fig. 1), with all moose home ranges located <30 km from a station. We obtained temperature data for moose in central Massachusetts from the Fisher Meteorological Station at Harvard Forest, where readings were recorded every 15 minutes, resulting in a maximum 7.5-minute difference between the time of temperature recording and the time of any moose GPS location (Boose 2001). Temperature data for western Massachusetts were obtained from weather station MAR 841 in Peru, Massachusetts (42.467171

N, 73.022499 W, 577 m) that used a Davis Instruments, Vantage Pro weather station. This weather station is part of the National Oceanic and Atmospheric Association (NOAA) MADIS (Meteorological Assimilation Data Ingest System) network. Temperature data at this station were recorded every 5 minutes.

We created subsets of the moose location data first by season, then day and night, and finally temperature class. We classified moose GPS locations as either day or night based on the time the location was recorded relative to sunrise and sunset (day was after sunrise and before sunset; night was after sunset and before sunrise). We obtained sunrise and sunset times from the website http://www.arachnoid.com/lutusp/sunrise/. We assigned GPS locations to the following ambient temperature classes relative to the seasonal UCT: cool ($<-5^o$ C in winter (early and late) or $<14^o$ C in spring, summer, and fall), warm ($\geq-5^o$ and $<0^o$ C in winter or $\geq14^o$ and $<20^o$ C in spring, summer, and fall), and hot ($\geq0^o$ and $<10^o$ C in winter or $\geq 20^o$ C in spring, summer, and fall). We used a fourth temperature class in winter: very hot ($\geq10^o$ C). For each season-day/night-temperature class combination, we calculated the mean proportional use of each vegetation cover type. Additionally, for each season we calculated the mean hourly proportional use of cover types and mean hourly movement rates.

1.4.3 Statistical Analyses

1.4.3.1 Thermal shelters

We used mixed effect analysis of variance, with block as the random intercept, to test for differences in daily maximum temperature among forest stand types using the R-package nlme (Pinheiro et al. 2013). For all analyses we subset the data by season, and combined early and late winter into a single season, winter. We accounted for the heterogeneity of variance between stands types by using the VarIndent command in nlme. Comparison of models with and without

modeled variance structure was based on Akaike Information Criteria (AIC) and likelihood ratio

tests (Burnham and Anderson 2004). Models that included the incorporation of variance

structure were better for all seasons (all $P < 0.001$). Additionally, data exploration indicated that

the temperature difference between stand types increased with increasing maximum daily

temperature. We modeled the maximum daily difference in temperature between stand types

compared to daily maximum temperature recorded at the Fisher Meteorological Station using

mixed effect linear regression. We modeled the heterogeneity of variance for various models

using fixed, power, and exponential variance structures and without modeling the variance

structure. Likelihood ratio tests and AIC were used to determine the best variance structure,

which was then used in the analysis. We used Bonferroni corrections to account for multiple

comparisons within season.

1.4.3.2 Proportional Use of Cover Types

Within each season and for day and night we used mixed effect analysis of variance to

compare the use of cover types across temperature classes, as well as overall daytime versus

nighttime use. We used a random intercept model for all analyses, with individual moose as the

random component, to account for repeated measures on an individual. Models were analyzed

with the package lme4 (Bates et al. 2012) and post-hoc comparisons and MCMC P-values were

calculated with the package languageR (Baayen 2011).

1.4.3.3 Resource Selection Functions (RSF)

We modeled how third-order habitat selection (Johnson 1980) was influenced by ambient

temperature and photo-period (day versus night) by calculating resource selection functions

(RSF) using a use:availability framework (Manly et al. 2002) and assuming the exponential form

(Johnson et al. 2006). We estimated model coefficients (β_i) representing the relative probability of use (w) using mixed effect logistic regression with the equation:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + ... + \beta_k x_k + y_i)$$

where y_i is the random effect of moose i.

We based availability for each animal on a random sample of locations generated within the animal's annual minimum convex polygon home range, plus a buffer to account for habitat available along the periphery of the home range. We used a 1,000 m buffer that was equivalent to the 95th quantile of between-location movements. We added the buffer around all locations then merged it with the MCP to define availability to represented habitat that was easily available to the individual. This sampling resulted in 1,175-1,527 random locations per individual. We classified the cover types for the random locations using the same method as for used locations. The availability data had no ambient temperatures associated with it; therefore, we generated temperature data for each moose and season by randomly drawing with replacement from the temperature data associated with that moose's GPS locations for that season. To insure that no available location was associated with a single temperature value we first duplicated the available dataset 5 times; as a result, each available location had 5 temperature values associated with it. Temperature data associated with the available locations varied by season, but availability of cover types was held constant for all analyses.

For all analyses, we used subsets of the data based on season and photo-period (e.g., summer daytime). Models for each subset included the categorical variable "cover type" and the continuous variable "ambient temperature", plus their interaction. We generated separate models for central and western Massachusetts because of differences in seasonal habitat selection due to differences in forest type and plant community composition (Wattles and DeStefano 2013a). We

used a random intercept model for all analyses, with individual moose as the random component, to account for repeated measures on an individual and unequal sample sizes (Gillies et al. 2006). We analyzed the models with the package lme4 (Bates et al. 2012). We evaluated the robustness of our models using k-fold cross validation (Boyce 2002), withholding 20% of the data to test models generated with the remaining 80%. This method generates Spearman's rank correlation coefficients (r_s), with high r_s indicative of good model fit. Finally, we used mixed effect analysis of variance to model differences in selection of cover types during the day versus at night.

1.5 Results

1.5.1 The Thermal Environment

1.5.1.1 Ambient Temperatures versus UCTs.

Daily minimum temperatures exceeded the lower (exponential increase in metabolism) UCTs on 66% or 38% days of the year (when -5° C or 14° C were used for spring and fall, respectively) (Table 2). The daily mean temperature exceeded these UCTs on 86% or 68% of days, respectively, and the daily maximum temperature exceeded these UCTs on 96% or 87% of days, respectively. When the maximum daily temperature exceeded the lower UCT, it did by an average of 6.8, 11.2, 6.8, 10.8, and 9.7^o C from spring to late winter. The longest period the daily minimum temperature stayed above the 14° C UCT was over 22 days, when the mean minimum and maximum temperatures were 17.9 and 28.9^o C, respectively. For that period, ambient temperatures were never within the thermal neutral zone of moose. During the same period, the daily minimum temperature remained above the 20° C threshold for over 4 days.

1.5.1.2 Heat Stress Indices

Comparison of Heat Stress Indices for Petersham, Massachusetts and northeast Minnesota revealed that the mean annual daily and seasonal HSIs were greater for Massachusetts than Minnesota (Table 3). Mean annual and daily HSI values for Late Spring and Warm Seasons were only 20-28% greater in Massachusetts than Minnesota, but were 193% greater during January and 73% greater during the overall Cold Season. However, 3 of 4 single year maxima HSI for the Late Spring and Warm Season periods were greater in Minnesota, indicating that Warm Season temperatures can be more extreme in the continental climate of Minnesota than the maritime climate of Massachusetts. Cold Season HSIs were always greater in Massachusetts, including January, the period Lenarz et al. (2009) determine had the greatest effect on moose survival.

1.5.1.3 Thermal Shelters

Daily maximum temperatures were greater in regenerating stands in all seasons than either mature hemlock or deciduous stands, and mature deciduous stands were greater than mature hemlock stands in all seasons (Table 4; all $P \leq 0.003$). The mean differences in maximum daily temperature between regenerating and hemlock stands ranged from 5.81 ($\pm$ 0.24)$^{\circ}$C ($\bar{x}$ ($\pm$ SE)) in summer to 3.19 ($\pm$ 0.26)$^{\circ}$C in winter. Additionally, the difference in maximum daily temperature between stand types increased with increasing daily maximum ambient temperature for most combinations of stands and seasons (Table 4, Fig 3, all $P < 0.001$; except for regeneration and deciduous in winter $P = 0.028$). The difference in temperature between deciduous and hemlock stands did not change with changes in daily maximum ambient temperature during fall ($P = 0.471$).

1.5.2 Moose Habitat Use and Thermoregulatory Behavior

1.5.2.1 Capture and Deployment of GPS Collars

We deployed GPS collars on 26 adult moose (7 females and 19 males). Of the 26, we excluded 5 from the analysis due to mortality, suspected infection with brainworm (*Parelaphostrongylus tenuis*), or collar failure, resulting in 21 collared moose (5 females and 8 males in central and 8 males in western Massachusetts). We recaptured and recollared 9 moose when the batteries in their initial GPS collars ran low. We obtained 127,408 locations of the 21 moose used in this study, with an overall fix rate of 85%. Seasonal data for any animal was only included in the analyses if data were obtained across the entire season. The median number of locations per animal per season ranged from 402 in spring to 1,015 in late winter. The minimum number of locations was 281 for one animal in spring.

1.5.2.2 Ambient Temperatures at GPS Locations

Temperatures experienced by collared moose in our study were consistently outside of their thermal neutral zone in all seasons both day and night (Table 5). During summer, temperatures were above the 14° C threshold for over 90% of daytime and 75% of nighttime locations and above the 20° C threshold for over 56% of daytime locations. During early and late winter, temperatures were above the -5° C threshold for 85 and 75% of daytime locations and for 76 and 57% of nighttime locations, respectively.

1.5.2.3 Proportional Habitat Use versus Ambient Temperatures

We combined males and females in central Massachusetts, as modeling results showed no differences between gender for habitat use and thermoregulatory behavior based on significance level and AIC (Figs. 4-7). In the central study area in spring, the proportional use ($\bar{x}$

(± SE)) of regeneration decreased from 0.545 (± 0.033) to 0.307 (± 0.033) to 0.231 (± 0.042) as

temperatures increased from cool (<14°) to warm (14-19° C) to hot ($\geq$20°), respectively, which

represented 44 and 58% decreased use of regeneration from cool to warm and cool to hot

temperatures, respectively. In summer, the proportional use of regeneration decreased from

0.650 (± 0.046) to 0.488 (± 0.052) to 0.352 (± 0.040), a 25 and 46% decrease in regeneration use

from cool to warm and cool to hot temperatures, respectively. In fall, use decreased from 0.484

(± 0.048) to 0.349 (± 0.045) to 0.282 (± 0.039), a 28 to 42 % decrease in regeneration use from

cool to warm and cool to hot temperatures, respectively. Additionally, use of regeneration was

48% greater during the night (0.612 ± 0.038) compared to the day (0.413 ± 0.031) in spring, 55%

greater during summer (0.663 ± 0.036 and 0.428 ± 0.043 for night and day, respectively), and

63% greater during fall (0.632 ± 0.027 and 0.387 ± 0.039 for night and day, respectively).

Comparatively, the use of wooded wetlands increased from 0.101 (± 0.014) to 0.332 (± 0.010) (a

228% increase), from 0.118 (± 0.026) to 0.295 (± 0.035) (a 150% increase), and from 0.189 (±

0.034) to 0.337 (± 0.053), (a 77% increase) from the cool to hot temperature class during spring,

summer, and fall, respectively (Fig. 3). Proportional use of mature forest stands, particularly

conifer, also increased with increasing temperature; however, the patterns were not consistent

season to season. In addition, the use of all thermal shelters, such as wooded wetlands and

mature forest stands, nearly doubled during the day compared to at night during these seasons.

Changes in the proportional use of regeneration in relation to UCT was less pronounced

in western Massachusetts in spring (0.199 (0.050) to 0.162 (0.052) to 0.165 (0.038) from cool to

warm and hot), when deciduous forest was used heavily, and in summer (0.470 (0.061) to 0.388

(0.059) to 0.342 (0.060) from cool to warm to hot) (Fig. 5). However, during fall changes in the

proportional use of regeneration were similar to central areas, decreasing from 0.417 (0.052) to

0.305 (0.052) to 0.245 (0.064) as temperature increased. Use of wooded wetlands doubled as

temperatures increased from cool to hot in spring (0.131 (0.018) to 0.254 (0.047)) and summer

(0.090 (0.033) to 0.191 (0.025)) and nearly tripled from cool to hot temperatures in fall (0.130

(0.031) to 0.367 (0.061)). The differences in use of cover types between day and night were

similar in summer and fall for central and western areas, but not as pronounced in the west

during spring.

Examination of the use of cover types versus hour of the day revealed a clear transition

from open cover types (particularly regenerating forest) to thermal shelters (most notably conifer

and wooded wetlands) occurring at dawn, with the reverse pattern at dusk (Figs. 8 and 9). The

transition in the use of cover types was matched by peaks in hourly movement rates during

crepuscular times (Fig. 10).

The magnitude of the decline in use of regeneration was much less at the identified UCTs

in early and late winter than in spring, summer, or fall. During the day in central Massachusetts,

use of regenerating forest stands decreased by only 5 and 7% from the cool ($<-5^o$ C) (0.534

(0.067) and 0.543 (0.050) in early and late winter, respectively) to warm ($\geq-5^o$ and $<0^o$ C)

((0.510 (0.067) and 0.505 (0.038) in early and late winter, respectively) temperature class and by

13 and 17% from the cool to hot ($\geq0^o$ and $< 10^o$ C) (0.467 (0.042) and 0.449 (0.038), in early and

late winter, respectively) temperature class in early and late winter, respectively (Fig. 6).

However, compared to cool temperatures the use of regeneration decreased by 45% in early

winter (to 0.295 (0.037)) and 44% in late winter (to 0.305 (0.047)) when temperatures were 10

degrees above the upper UCT (very hot). Notably, the decrease in use of regeneration was also

significant between both warm and very hot ($>10^o$ C) and hot and very hot temperatures.

Similarly, the change in the use of cover types at night versus day was also much lower in early and late winter than during spring, summer, and fall.

1.5.2.4 Resource Selection versus Ambient Temperatures

The analysis of habitat selection with RSFs showed that the relative selection for regenerating forest was several times the selection for all other cover types at low temperatures. As temperature increased the relative selection for regenerating forest decreased in spring, summer, and fall in central Massachusetts, with the decrease more pronounced during the day than at night (Fig. 11, Appendix A). At night, selection for regenerating forest remained high relative to closed canopy forest types, even at high temperatures. During the day, however, selection for regenerating forest was comparable to closed canopy forest at high temperatures. Relative selection for wooded wetlands increased rapidly with increasing temperature both day and night and was several times greater than all cover types, even regenerating forests at high temperatures. To a much lesser extent, selection for other wetlands and conifer also increased during the day. At night, the selection for open wetland types increased much more rapidly with increasing temperature and was similar in magnitude to the increase in selection for wooded wetlands. Similarly to proportional use, selection ratios at night and day showed increased selection of regenerating forest and lower selection for thermal shelters at night compared to day.

In western Massachusetts, selection for regenerating forest declined with increasing temperature during the day in spring, summer, and fall (Fig. 12, Appendix B). Selection for regeneration also decreased with increasing temperatures at night during fall, but not at night during spring and summer. Selection for deciduous forest (the most heavily used cover type in spring) declined during both day and night as temperature increased. Similarly, during summer selection for other wetlands decreased as temperatures increased, both day and night. Wooded

wetlands remained the most heavily selected for thermal shelter during the day and selection for this cover type was several times that of other cover types at high temperatures. Selection of other wetlands also increased with higher temperatures at night during both spring and fall.

In central Massachusetts, selection for regeneration was high during winter, but decreased with increasing temperature during the day in both early and late winter (Fig. 13). At night relative selection for regeneration remained high even at seasonally very high temperatures and decreased less with increasing temperature than during the day. Selection for wooded wetlands increased rapidly with increasing temperature at both day and night, but relative selection remained below regeneration until temperatures were above the 0° C UCT. Differences in selection pattern complicated the results in western Massachusetts; however, the increase in selection for wooded wetlands with increasing temperature demonstrates its continued importance as a thermal shelter (Fig. 14).

K-fold cross validation showed excellent predictive performance of the models for all seasons in both study areas with $r_s = 0.97$ (0.95 - 0.995) for central and 0.95 (0.92 - 0.98) for western models.

1.6 Discussion

1.6.1 A Critical Evaluation of UCTs for Moose

Although the UCTs reported by Renecker and Hudson (1986) have been widely cited, there is also reason to be cautious with their results. They identified UCTs for moose based on a small sample ($n = 2$) of captive animals in one specific region of the species geographic range. As a result of the limitations of that study, several authors (van Beest et al. 2012, Broders et al. 2012, McGraw et al. 2012, McCann et al. 2013, Melin et al. 2014) have cited the lack of thermoregulatory behavior by moose at the identified UCTs in Ontario (Lowe et al. 2010), as

evidence that either (1) moose response to temperature is variable across their southern range or (2) the UCTs identified by Renecker and Hudson are inaccurate or inappropriate across the range.

However, while it is possible that moose in southern Ontario did not respond to the thermal environment, it is also highly probable that the coarse-grained analysis used by Lowe et al. (2010) would not have detected any thermoregulatory behaviors even had they been present. GIS layers commonly used to represent habitat availability often have associated error due to misclassification of cover types and blurred boundaries due to low resolution. In fact, Maxie et al. (2010) reported large inaccuracies in the GIS forest map used in the analysis in Ontario, and cautioned that its use may be inappropriate for many wildlife studies. Lowe et al. (2010) also used utilization distributions to represent habitat use, a smoothing method that removes the fine spatial resolution of animal location data that GPS collars provide. Finally, they merged early successional forest with mature forest types, did not distinguish between open and forested wetlands, and did not account for night versus daytime use. Alone each one of these factors would tend to dampen the patterns in the data; in combination, they likely smoothed all patterns out of the data.

Lowe et al. (2010) also failed to detect differences in movement rates among temperature classes or between day and night, which they interpreted as a lack of changes in behavior at high temperatures and a lack of increased nocturnal activity. We performed an exploratory analysis of movement rates versus temperatures and did not see any clear relationship, despite the clear patterns of thermoregulatory behavior and habitat use we observed. Furthermore, our observed movement rates were similar during the day (when moose were using thermal shelters) and night (when moose were foraging in regenerating stands). These results indicate that, despite the fine

spatial and temporal resolution of GPS collars, they do not have the ability to detect differences in within patch activity or foraging versus bedding based on movement rates.

The preponderance of evidence from our and other studies suggests that moose are affected by and respond to high temperatures with thermoregulatory behavior at the temperatures proposed by Renecker and Hudson (1986) (Renecker and Hudson 1990, Schwabb and Pitt 1991, Demarchi and Bunnell 1995, Dussault et al. 2004, Broders et al. 2012, van Beest et al. 2012, Melin et al. 2014). Additionally, McCann et al. (2013) reported physiological responses to heat stress at a mean of 17° C in summer, confirming the temperatures Renecker and Hudson (1986) reported. This result supports the idea that there is a range of temperatures where individual moose will begin to experience thermal stress (Renecker and Hudson 1986, Renecker and Hudson 1990, McGraw et al. 2012). In fact, Renecker and Hudson (1986:326) reported that "upper thermal limits were found to be 14-20° C", i.e., that range is bounded by their observed 14° C exponential increase in metabolic rate and 20° C open mouthed panting temperatures. As such, temperatures between 14 and 20° C should be interpreted as the range where thermal stress begins to occur, and temperatures above 20° C could be interpreted as well above the thermal neutral zone of moose. We are thus confident that using the upper critical temperatures reported by Renecker and Hudson (1986) to represent thermally stressful conditions for moose is valid.

1.6.2 The Thermal Environment of Southern New England

1.6.2.1 Temperatures Relative to UCTs

Comparison of mean daily minimum, maximum, and mean temperatures to seasonal UCTs indicated that moose were subjected to thermally stressful conditions frequently and for long periods throughout the year in Massachusetts. Maximum daily temperatures exceeded the lower UCT thresholds of -5 and 14° C on nearly 90% of the days of the year. Perhaps more

importantly, minimum daily temperatures often exceeded the lower UCT as well, and on these days ambient temperatures were never within the thermal neutral zone of moose. Furthermore, conditions outside the thermal neutral zone lasted for extended periods, often days and weeks at a time, particularly during summer.

1.6.2.2 Factors Affecting the Thermal Environment

Climatic conditions so consistently outside the physiological tolerances of moose would seemingly put Massachusetts and southern New England outside the suitable geographic range for moose. However, many factors can modify the thermal environment experienced by an animal, including vegetation cover, convective and conductive cooling, and exposure to solar radiation.

Vegetation cover can have a large modifying effect on the thermal environment. Closed canopy forest can be cooler than more open habitats and can reduce exposure to solar radiation, which can have a dramatic effect on operative temperature. Parker and Gillingham (1990) suggested that operative temperature of an animal in cover may be 20° C cooler than ambient temperature due to the reduction in solar radiation. Demarchi and Bunnell (1993) stated that canopy closure of 26-35, 36-45, 66-75, and 76-85% allowed moose to remain below or near their UCT at temperatures of 15°, 20°, 25°, and 30° C, respectively. Bowyer and Kie (2009) found black body temperatures in open habitats to be over 10° C warmer than ambient temperature or in oak cover during the day, but cooler at night.

We detected maximum temperature differences between open regenerating stands and closed canopy hemlock or deciduous stands of nearly 6° C in summer. Similarly, in Oregon Edgerton and McConnell (1976) reported that during summer mean hourly temperatures between clearcuts and adjacent unlogged conifer and partial cut stands differed by up to 7-8° C. In

Minnesota, McGraw et al. (2012) reported that differences in temperature among forest cover types increased with increasing temperature and was greatest in the afternoon, which is typically the warmest part of the day. They also found that temperatures were considerably lower ($\sim5^{\circ}$ C) and the differences between stand types were less on cloudy versus sunny days. We report very similar results, indicating that the value of vegetation cover as thermal shelter increases on warmer and sunnier days when it is needed most.

Wooded wetlands provide the cover benefits associated with closed canopy forests, including lower ambient temperature and reduced solar radiation, as well as and perhaps more importantly, a medium for conductive cooling with water. Renecker and Hundson (1990) reported that bedding in shallow water decreased energy expenditure by 2.9 kJ/hr/kg$^{0.75}$ from the daytime average and decreased respiration from 26 breaths/min when bedded in the shade to 7.5 breaths/min when bedded in a shallow wetland. Just standing in a shallow wetland decreased energy expenditure by 6.52 kJ/hr/kg$^{0.75}$ compared to an animal standing in willow (*Salix* spp.). Demarchi and Bunnell (1995) and Parker and Gillingham (1990) noted that large animals have high thermal inertia, and their low surface area-to-volume ratio results in low rates of heat transfer to and from the animal or environment. As a result, animals like moose are slow to heat up when exposed to high temperatures and solar radiation. However, once they are outside of their thermal neutral zone it can take a long time to cool down. The use of wetlands can help to accelerate this cooling or halt and reverse thermal inertia. This could enable moose to spend time in regenerating forest when conditions were unfavorable, followed by rapid cooling in wetlands to quickly reduce body temperature. Ackerman (1987) and Renecker and Hudson (1990) noted that moose used wetlands as heat sinks in summer.

Convective cooling by air movements can also have a strong influence on the rate of energy exchange between an animal and its environment. Strong winds can quickly move warmth from a body and greatly accelerate cooling. McCann et al. (2013) determined that exposure to wind raised the ambient temperature where moose began to experience increased metabolic rates by 4-10 ^{o} C. Parker and Gillingham (1990) modeled how the operative temperature for mule deer (*Odocoileus hemionus*) was affected by air temperature, solar radiation, and wind speed. At 15° C and maximum solar radiation, winds of 0, 5, 10, and 15 m/s resulted in operative temperatures of 40.5, 23.9, 16.7, and 11.2^o C, respectively. Conversely, at 15° C and no wind, solar radiation of 0, 200, 400, 600, and 800 W/m^2 resulted in modeled operative temperatures of 11.0, 20.7, 29.7, 38.4, and 40.5^o C, respectively. Elevation and topography can influence the thermal environment by changing the exposure to wind. Elevation can also directly affect the thermal environment through adiabatic cooling, approximately 1° C for every 100m in altitude in dry air (0.6^o C in moist air) (Begon et al. 2006).

1.6.3 Moose Habitat Use and Thermoregulatory Behavior

1.6.3.1 Habitat Use

Our results clearly indicate that moose in Massachusetts are living in an environment that is consistently outside their thermal neutral zone. Moose responded to these conditions by performing thermoregulatory behaviors, including altering their use of cover types and daily activity patterns, related to both temperature and time of day. Moose used more open regenerating forest that optimized foraging efficiency when conditions were favorable (e.g., at low temperatures and at night). Conversely, they greatly reduced use of open foraging habitat and increased their use of thermally advantageous forested wetlands and closed canopy forests as temperatures increased and during the day.

Proportional use analysis showed that moose responded to temperature at the identified UCTs, particularly during spring, summer, and fall, indicating heat stress was occurring at the temperatures identified by Renecker and Hudson (1986). The decreased use of open habitats and increased use of cover, particularly conifers or softwoods, when summer temperatures were above the UCTs were also reported for moose in British Columbia (Schwabb and Pitt 1991, Demarchi and Bunnell 1995), Quebec (Dussault et al. 2004), Nova Scotia (Broders et al. 2012), Norway (van Beest et al. 2012), and Finland (Melin et al. 2014). However, the magnitude of the response we observed was far greater, as would be expected given the location of Massachusetts in the range of moose and the thermal conditions relative to other locations where these interactions have been studied (Table 6).

Our habitat selection analysis also revealed important insights into the energy balance of moose. Specifically, by incorporating temperature as a continuous variable in our models, we were able to identify the seasonal temperatures where moose switched between selecting for stands with high forage density that maximized energy consumption, to where it is more efficient to conserve energy through the selection of thermal shelters. At temperatures above this transition temperature, more energy would likely be expended to maintain normal body temperature than could be obtained through foraging. This pattern was much clearer in central Massachusetts, where regenerating forests were the most heavily used cover type in all seasons. In western Massachusetts, selection was complicated by the variability in seasonal habitat selection patterns related to differences in forest type between central and western Massachusetts (Wattles and DeStefano 2013a).

During the day in central Massachusetts, the transition temperature was about 12° C in spring, 16° C in summer, and 6° C in fall. At night, transitions temperatures were about 5° C

warmer and likely reflected the impact of solar radiation on the heat exchange of an animal. The transition occurred at similar temperatures in western Massachusetts, except in spring when moose selected deciduous forest stands that provided both cover and forage. If the selection for the two main foraging habitats, which were deciduous and regenerating stands, were combined, the transition occurred near 15° C. The temperatures these transitions occur at further supports the accuracy of the 14° C summer UCT originally defined by Renecker and Hudson (1986) and confirmed by McCann et al. (2013). Additionally, the relative temperature of the transition between seasons supports the hypothesis that moose are most susceptible to thermal stress in spring, when they are shedding their winter coat and are in poor body condition, and in fall, when they are developing their winter coat and animals are expending energy during the active rutting period. Melin et al. (2014) suggested the greater use of cover at high temperatures, which they observed in August compared to June or July, was related to the development of the winter coat at that time.

The response to temperature was much lower in winter than in the warm seasons. Based on proportional use analysis, moose did not appear to respond to temperature at the identified UCT in winter, which is in agreement with much of the literature. Van Beest et al. (2012) did not detect thermoregulatory behavior in winter in Norway and stated that most other studies did not detect changes in winter selection (except see Scwabb and Pitt 1991). Additionally, comparison of both overall night versus day use and hourly use of cover types revealed that the response to time of day was also greatly reduced in winter, which is not surprising given the much-reduced intensity of solar radiation at this time of year. However, we did see significant changes in the use of cover types when temperatures exceeded the upper UCT by 10° C in winter.

The lack of thermoregulatory response in winter at the identified UCTs indicated that perhaps the UCTs for winter are not as accurate or applicable across the species' range as the summer UCTs. However, with the lack of deciduous cover (i.e., leaves are down) and lower ambient temperatures in winter, it may be that the differences in thermal conditions between cover types are not great enough to warrant the same level of thermoregulatory behavior that we observed during the warm seasons, even under thermally stressful conditions, except at the very highest temperatures. Furthermore, bedding in snow during warm temperatures likely provides some cooling effect regardless of cover type. The lack of response at the UCT may also reflect the interaction of solar radiation and ambient temperature in the heat exchange of animals. Without the high intensity solar radiation that occurs during spring, summer, and fall, ambient temperature alone may not result in thermal stress. However, we did see an increase in the use and selection of wooded wetlands as temperatures increased in winter, indicating that thermal stress was occurring.

Incorporating additional variables such as wind speed, elevation, aspect, cloud cover or intensity of solar radiation, and precipitation, all of which could modify the thermal environment, would undoubtedly improve models of animal response to the thermal environment. Likely some use of open habitats when temperatures were above the UCTs occurred under cloudy, windy, or rainy conditions, which lowered an animal's operative temperature and confounded the habitat selection-temperature relationships we modeled. The strength of the relationships between habitat selection and temperature and the magnitude of the changes in habitat use with changing temperature, despite this source of environmental variation, are compelling evidence that ambient temperature is a main driver of habitat selection for moose along their southern range boundary. The difficulty in accurately modeling wind, cloud cover, and precipitation, given

changes in locality, as well as the effects of elevation, aspect, slope, and cover, make accurately incorporating these variables extremely difficult. However, during this study moose were located almost exclusively in the uplands of the study area. This may have involved a home-range scale selection for lower temperatures and greater exposure to wind in the uplands or it may be avoidance of the more highly developed valley bottoms (Wattles and DeStefano 2013b, see also chapter 3). We believe it is likely combination of these two factors.

1.6.3.2 Activity

In addition to altering their habitat use and selection patterns in response to thermal conditions, moose also modified their activity patterns. Moose in our study were highly nocturnal in spring, summer, and fall, intensively using regenerating stands and to a lesser extent open wetlands at night. We documented a clear shift in the use of open regenerating habitat and thermal shelters that occurred at dawn and dusk, coupled with peaks in movement rates at these times. We interpreted this as a shift in activity from primarily resting and bedding during the day to foraging at night. Additionally, the peaks in movement rates that we observed at dawn and dusk represented movements between foraging and cover patches, not simply peaks in foraging activity, as is normally interpreted (Belovsky and Jordan 1978, Renecker and Hudson 1989, Neumann et al. 2012). At night, moose used regenerating forest extensively to feed, but their rates of movements during this time were low and similar to the rates they showed when in thermal shelters during the day. However, moose likely performed feeding bouts just prior to entering and after leaving thermal shelters at dawn and dusk, respectively.

Increased nocturnal activity and reduced foraging time and activity with increasing temperature are commonly reported for moose in the literature. Belovsky and Jordan (1978) stated that moose are primarily nocturnal during summer, with peaks in activity at dawn and

dusk, and reference Knorre (1959), who claimed a nocturnal activity pattern. Renecker and Hudson (1989) reported highest levels of foraging at dawn and dusk, but noted increased nocturnal foraging in late spring and summer. A biphasic activity pattern with peaks at dusk and dawn is commonly reported during the growing season (Cederlund 1989 and references therein), but not during winter. However, Cederlund (1989) noted that their activity measurements were recorded remotely and only distinguished between active and inactive, which could represent any movement and not necessarily increased foraging behavior.

Nocturnal activity combined with reduced feeding as temperatures increased lead Belovsky and Jordan (1978) to speculate that moose limited their activity due to thermal conditions, and that high temperatures could restrict forage intake. Moen (1968) noted that both activity and food consumption increase metabolic heat production several times basal metabolism; given this, it is not surprising moose reduce activity during the day. Cederlund (1989) reported shorter and more frequent activity bouts, which he believed to be an attempt to maximize forage intake during the growing season. Van Ballenberghe and Miquelle (1990:395) also noted a decrease in the length of activity bouts during mid-day that "appeared to be related to temperature". Ackerman (1987) and Broders et al. (2012) reported reduced movement rates at high compared to low temperatures. However, we were unable to detect a relationship between movement rates and ambient temperature. Renecker and Hudson (1986) and Demarchi and Bunnell (1995) both described decreased activity with increasing temperature. Dussault et al. (2004) reported higher activity by moose during the day than night in all seasons; however, they also reported that nocturnal activity increased with warmer temperatures in summer and fall.

1.6.4 Impacts of Temperatures Above UCTs

Conditions outside the thermal neutral zone can affect the energy budget of an animal by decreasing inputs and increasing expenditures. Renecker and Hudson (1992:54) stated, "thermal stress preempted feeding when ambient temperatures rose above 0° C in winter and 22° C in summer". Reduced time feeding (Knorre 1959, Belovsky and Jordan 1987, and Renecker and Hudson 1986, Schwabb and Pitt 1991) and reduced dry matter intake (Renecker and Hudson 1990) that resulted in associated static weight or weight loss (Renecker and Hudson 1986) or reduced weight gain (Knorre 1959) during periods of high temperature are widely reported. At the same time, physiological responses (Renecker and Hudson 1986) to maintain normal body temperature are a direct energy expenditure. Thermal panting is energetically costly and increases in metabolic rate are, by definition, a greater expenditure of energy. Therefore, when temperatures exceed UCTs moose expend energy that they would not have to in a thermally neutral environment. In Massachusetts, the 11.2^o C average that daily maximum temperatures exceeded the 14° C UCT by in summer would result in an increase in metabolic rate of 7.8 kJ/hour/kg $BW^{-0.75}$, an increase in heart rate of 10 beats/minute, and an increase in respiration rate of 35.8 breaths/minute compared to temperatures below the threshold.

Belovsky and Jordan (1978) stated that summer was the most nutritionally demanding season because moose need to raise young and store fat for winter. Van Ballenberghe and Miquelle (1990:392) also believed that summer is the most important time of year, when fat and protein stores are replenished and that "the size of those stores determines how long animals survive in a negative energy balance during winter". Given the importance of the season in the annual energy balance of moose, periods above the UCT in summer are likely extremely costly. If thermal stress during the growing season reduced energy reserves going into winter, then

presumably the probability of survival would decrease. During the day in summer, we observed high use of regenerating forest even at temperatures above 20° C. This likely reflected the almost continuous state of temperatures outside of the thermal neutral zone during summer (98% of daytime locations) and the necessity to feed at this critical time of year regardless of the metabolic energy required to do so.

Iason et al. (1999) showed that domestic sheep were able to compensate for restricted grazing times by increasing their instantaneous foraging rates and increasing the length of their foraging bouts. However, they could only offset the restrictions in grazing time when food was abundant. Foraging in lower quality habitat resulted in a reduction in daily food intake compared to sheep allowed unrestricted grazing. Presumably, the short passage and digestion times of summer vegetation may allow moose to compensate for reduced food intake during periods of thermal stress through the intensive use of high quality regenerating forest on cooler days (Renecker and Hudson 1992) or at night. However, the use of thermal shelters may result in decreased energy consumption because they represent lower quality foraging habitat.

The use of thermal shelters and thermoregulatory behavior may allow moose to minimize the energy expenditure required to maintain body temperature. However, the use of thermal shelters does not automatically confer a thermally neutral and therefore energetically neutral environment. We observed a large bull bedded in the shade at a time when there was a moderate breeze and an ambient temperature of about 24° C; he was breathing at a rate of over 60 breaths/minute, about 10 times the rate expected at temperatures below the UCT (Renecker and Hudson 1986). Nevertheless, given the reduced metabolic rates reported by Renecker and Hudson (1990) for moose standing in shallow water compared to a standing in willow (6.5 kJ/hr/kg$^{0.75}$), thermal shelters can minimize energetic costs. For a 275 kg (600 pound) moose,

this represents a savings of approximately 439 kJ or the equivalent of 105 kilocalories per hour spent in a wetland compared to using a regenerating stand. The large thermoregulatory benefits of bedding or standing in water are apparent in the very high use and selection for wooded wetlands at increasing temperatures that we observed.

Regardless, whenever temperatures exceed the UCT moose must make a choice whether to maximize foraging in open habitats at the expense of greater metabolic energy expenditure or to minimize energy expenditure by using thermal shelters at the expense of foraging efficiency or even feeding at all. Irrespective of the choice, the result is a decrease in stored energy compared to more favorable thermal conditions. In terms of the energy balance of an individual, this energy must be compensated for at another point, or the result will be a net negative energy balance. As a result, greater time outside an animals' thermal neutral zone can lead to declines in body condition, potentially greater susceptibility to disease, parasites, and predators, lower body reserves for winter, and overall declines in survival and reproduction (Murray et al. 2006; Lenarz et al. 2009, 2010).

1.6.5 Heat Stress Index

Despite documenting nearly 50% reductions in the daytime use of optimal foraging habitat, we were unable to quantify the energetic costs associated with conditions outside the thermal neutral zone or determine the cost or benefits of performing the thermoregulatory behaviors we observed in our GPS collared moose. Further, we did not determine how these environmental conditions affected moose body condition, reproduction, or survival. However, high temperatures and periods outside the thermal neutral zone of moose have been determined to negatively affect survival in Minnesota (Murray et al. 2006; Lenarz et al. 2009, 2010, however

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see Mech and Fieberg 2014). We compared temperatures experienced by moose in Massachusetts to those in Minnesota to extrapolate potential impacts.

We compared temperatures relative to seasonal UCTs and a HSI calculated for both areas: this analysis revealed that moose in southern New England were subjected to conditions outside of their thermal neutral zone more often and for longer periods than in Minnesota (Lenarz et al. 2009, McGraw 2012). This, combined with the strong negative correlation between the Minnesota HSI and moose survival (Lenarz et al. 2009), would lead one to predict that moose survival in Massachusetts would be similarly if not more negatively impacted. This might be especially true in light of Lenarz et al.'s (2009) conclusion that temperatures outside the thermal neutral zone in January and the overall Cold Season had the greatest effect on survival; the HSIs in Massachusetts were 193% greater in January and 78% greater in the Cold Season than Minnesota.

However, we did not see drastic thermoregulatory behaviors at high temperatures in winter, indicating heat stress was not a major issue at that time. Additionally, we do not suspect a large decline in the population in Massachusetts (Wattles and DeStefano 2011, Massachusetts Division of Fisheries & Wildlife unpublished data) as has been documented in Minnesota (Murray et al. 2006; Lenarz et al. 2009, 2010). This suggests that many factors other than temperature, such as habitat configuration and quality, predators, parasites and diseases, and moose density, all additively contribute to moose body condition and survival (Murray et al. 2006).

It may be that the actual day-to-day patterns in weather, including the range of daily, seasonal, and annual temperatures, may influence the impacts of thermal stress on moose. The continental climate of Minnesota leads to larger differences in seasonal temperature than the

maritime climate of Massachusetts. Winter temperatures in Minnesota are typically much colder (January mean maximum -10.2°C and minimum -23.1°C) than Massachusetts (0.5°C and -10.7°C; PRISM Climate Group 2013), whereas summer temperatures are much more similar (July 24.9°C and 11.6°C and 27.3°C and 14.9°C, for Minnesota and Massachusetts, respectively; PRISM Climate Group 2013). The narrower range of temperatures in Massachusetts could potentially limit the impacts caused by high temperatures, as the necessity to be able to cope with the extreme cold during winter in Minnesota may prevent moose there from adapting physiologically to warmer temperatures. Additionally, the typically colder conditions in Minnesota mean that when temperatures do exceed the winter UCTs, that those temperatures represent a greater deviation from the norm; this in turn could cause greater thermal stress than the same conditions in Massachusetts. In general, the more consistent maritime climate of Massachusetts may limit the impacts of heat stress despite the overall warmer environment.

1.6.6 Climate Change, Range Shift, and Edge of Range

A species geographic range or distribution is defined by the set of conditions and resources that individuals require and can tolerate, all of which combine to affect energy balance and fitness (i.e., the ability to survive and reproduce) (Hall et al. 1992, Gaston 2003, Begon et al. 2006). Outside of the range, one or more conditions, past or present, exist that prevent successful occupation of that area. Given the presence of other requirements and absences of conditions and factors that prevent occupation by a species, the thermal environment of an area (including mean and extreme temperatures) can determine suitability of the area and can be a limiting factor for both homeotherms and heterotherms. Gradational changes in climate or the thermal environment toward the periphery of a species' range should result in a ramp or decrease in animal density and body condition as environmental conditions move closer to physiological limits and further

from a species' "ideal" (the thermal neutral zone), which is normally closer to the core of the range (Caughley et al. 1988, Hall et al. 1992).

However, species distributions or fundamental niches are defined by a multitude of interacting components of the environment, with temperature being but one of them. Our results clearly elucidate the complexity in modeling species distributions based on a single factor, such as with thermal envelope modeling (Pearson and Dawson 2003, Hampe 2004). Differences in the availability, distribution, and quality of suitable food, cover, and water, and the abundance and distribution of parasites, disease, and predators can all influence a species' energy balance and ability to cope with a set of thermal conditions. These factors combine to determine the realized versus fundamental niche of a species. The apparent unsuitability of the thermal environment of Massachusetts would theoretically exclude it from a modeled species distribution; however, moose have occupied the state for the past several decades, are reproducing, and are currently adapted to the environment.

There is little evidence that the moose population in Massachusetts is currently in severe decline. However, population level monitoring is difficult in our region and limited to indices of abundance such as reported moose-vehicle-collisions and moose sightings by deer hunters. As such, confidence in the accuracy of population estimates is low. Given those limitations, we do believe the initial exponential growth of the population following reoccupation of the region appears to have leveled off and the population seems to be stabilizing at the current level (Wattles and DeStefano 2011, U. S. Geological Survey and Massachusetts Division of Fisheries & Wildlife unpublished data). The influence of thermal stress on moose survival and reproduction may be one reason for the apparent lack of further growth in the population.

Moose have shown that they are able to cope with the existing thermal environment in southern New England by altering their habitat selection and activity patterns. However, regional climate models for the northeastern United States predict that seasonal temperatures in Massachusetts will increase by 3.1-3.2^o, 2.1-2.2^o, 2.5-2.7^o, and 2.5-2.6^o C in winter, spring, summer, and fall, respectively, for the period 2041-2070 compared to 1971-2000 (Rawlins et al. 2012). This will likely result in an increase in the frequency, duration, and magnitude of temperature events outside of the thermal neutral zone for moose. Whether moose will continue to be successful given this additional demand on their energy balance remains to be seen. We may already be observing a northward range shift of moose in the upper mid-western United States, and it is not hard to imagine a similar scenario unfolding in Massachusetts and southern New England under predicted climate change scenarios.

1.7 Management Implications

This study revealed how unfavorable the thermal environment in Massachusetts is for moose; however, it also reveals how moose have adapted to the environment by altering their activity patterns and through the selective use of cover types. Habitat configurations that allow moose to find high quality forage (early successional forest) and thermal cover (closed canopy forest and wooded wetlands) in close proximity are likely the main reasons moose have been able to survive in a climatic environment that would seem to be highly unsuitable to the species. Habitat quality is likely to become even more important for the long-term survival of moose in southern New England if predicted climate impacts do occur (Rawlins et al. 2012).

The continuous creation of early successional habitat through logging and protection of wetlands are essential to maintain this favorable habitat configuration. Logging is the only significant means of creating young forest in Massachusetts. Given the fine energy balance

moose experience in Massachusetts and their clear heavy selection of this cover type, its importance as foraging habitat cannot be overstated. These stands allow moose to maximize their forage intake over short periods with minimal energy expenditure due to the high stem density they provide, and in this way help to minimize exposure to harsh thermal conditions. Use of regenerating stands may allow moose to compensate for reduced foraging time caused by conditions outside their thermal neutral zone; something that lower quality foraging habitat may not provide (Iason et al. 1999). This is extremely important given the large expected costs that high temperatures have on the energy balance of moose in Massachusetts. Additionally, the typical style of logging in Massachusetts, which results in small cuts of limited intensity, produces regeneration in close proximity to forest edges or within partially closed canopy, further facilitating thermoregulatory behavior by moose.

However, declines in body condition caused by the direct impact of high temperatures and thermal stress on the energy balance of moose could result in reduced survival and productivity. Declines in body condition can lead to immunosuppression and greater susceptibility to parasites and diseases, which can further impact the energy reserves of individuals (Murray et al. 2006). McCann et al. (2013) also suggested that sick and diseased animals experience the effects of thermal stress at lower temperatures than healthy animals, suggesting a reinforcing cycle between thermal stress, immunosuppression, and parasites and diseases. Furthermore, warmer temperatures may provide conditions that are favorable to the survival and spread of some parasites (e.g., winter tick [*Dermacentor albipictus*], Bergeron et al. 2014).

Our results, along with the growing body of literature on moose-temperature relationships (Renecker and Hudson 1986, 1989, 1990, 1992; Ackerman 1987; Dussault et al. 2004; Murray et

al. 2006; Lenarz et al. 2009; Broders et al. 2012; van Beest et a. 2013; McCann et al. 2013, Melin et al. 2014), support the theory that high temperatures resulting in thermal stress are a limiting factor for moose and one, if not the main, factor delineating the southern range boundary of the species (Kelsal and Telfer 1974, Telfer 1984, Renecker and Hudson 1986, Karns 1997, Peek and Morris 1998).

Recent declines in moose populations across the southern range edge in North America, including in Minnesota (Murray et al. 2006; Lenarz et al. 2009, 2010), New Hampshire, Montana (DeCesare et al. 2014), and Nova Scotia (Broders 2012), have been linked with warming temperature. However, wolves and winter ticks are two factors that increasingly appear to have major impacts on these moose populations. Evidence from Minnesota indicates that wolves are having a strong influence on moose survival and population structure (Mech and Fieberg 2014, Minnesota DNR unpublished data). Mech and Fieberg (2014) reanalyzed the data from Lenarz et al. (2009) and reported that increasing wolf numbers, not thermal stress, may be driving the decline in Minnesota. In New Hampshire and Maine, studies initiated in 2014 have shown very high mortality rates, particularly in calves, that are preliminarily being attributed to winter ticks (New Hampshire Department of Fish and Game, unpublished data; Maine Department of Inland Fisheries and Wildlife, unpublished data).

Most likely, the impacts of high temperatures on moose body condition work additively with parasites, disease, habitat degradation, predators, winter severity, and other factors in affecting the energy balance of individual moose and moose populations in these areas. As these declines have occurred in recently healthy populations, it may be that increasingly unfavorable thermal conditions along the edge of the range are pushing these environments outside the physiological tolerances and suitable range of moose, making moose less able to cope with

parasites and other factors that they otherwise could in a more thermally neutral environment. As a result, we may be observing a gradual range shift, as moose densities decline and local populations disappear entirely along the southern periphery of the species' range. Where these range contractions occur will likely depend on the interaction of thermally stressful conditions and the presence or absence of other additive factors. For example, the absence of the main predators of moose in Massachusetts, wolves (*Canis lupus*) and brown bears (*Ursus arctos*), eliminates one factor that affects moose energy balances and populations dynamics elsewhere.

Tables

Table 1.1 Seasons used for calculating seasonal thermal stress and thermoregulatory behaviors in moose in Massachusetts.

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

Table 1.2 Mean percentage of days per season that the mean daily minimum, mean, and maximum temperatures in central Massachusetts exceeded the established thermal stress thresholds for moose (increased metabolic rates, -5 and 14° C, and open mouthed panting, 0 and 20° C, for winter and summer, respectively; Renecker and Hudson 1986). Data from 2002-2008. Season lengths are 104, 47, 92, 61, and 61 days for late winter, spring, summer, fall, and early winter, respectively.

	Minimum Temperature				Mean Temperature				Maximum Temperature			
	5°C	0°C	14°C	20°C	5°C	0°C	14°C	20°C	5°C	0°C	14°C	20°C
Late Winter	44.2	13.4	0	0	69.8	38.4	<1	0	88.0	66.3	7.2	1.3
Spring	100	91.1	4.3	0.0	100	100	29.8	4.0	100	100	70.9	36.8
Summer	NA	NA	53.4	4.2	NA	NA	91.2	43.3	NA	NA	98.7	88.5
Fall	100	89.5	10.0	0	100	100	42.6	5.6	100	100	73.6	41.6
Early Winter	61.1	25.7	0	0	83.1	54.1	1.0	0	95.6	79.2	9.8	1.0

Table 1.3 Comparison of a heat stress index (HSI) for central Massachusetts and northeastern Minnesota. HSI calculated after Lenarz et al. 2009. Data for Minnesota reproduced from Lenarz et al. 2009.

Physiologic Threshold	Season	Location	Daily Ambient Temp	Mean Annual HSI	Mean HSI/day	Min	Max
14 C	Late Spring (Apr-May)	Massachusetts	Max	239.8	3.9	167.8	290.3
			Min	1.9		0	6
		Minnesota	Max	189	3.1	45	360
			Min	1		0	3
	Warm Season (Apr-Oct)	Massachusetts	Max	1,590.4	7.4	1,472.8	1,704.2
			Min	168.6	0.8	127.8	232.8
		Minnesota	Max	1,329	6.2	873	1572
			Min	64	0.3	19	123
20 C	Late Spring (Apr-May)	Massachusetts	Max	72.7	1.2	30.9	108.1
			Min	0		0	0
		Minnesota	Max	57	0.9	4	141
			Min	0		0	0

	Warm Season (Apr-Oct)	Massachusetts	Max	679.9	3.2	605.4	787.1
			Min	2.7		0.8	5
		Minnesota	Max	552	2.6	253	793
			Min	2		0	9
-5 C	Jan	Massachusetts	Max	170	5.5	57.3	278.7
			Min	37.6	1.2	6.5	64.8
		Minnesota	Max	58	1.9	11	152
			Min	6	0.2	0	13
	Cold Season (Nov-Mar)	Massachusetts	Max	1350	8.9	1095.6	1680
			Min	334.3	2.2	225.3	460.2
		Minnesota	Max	779	5.2	618	1010
			Min	118	0.8	86	160

Table 1.i a: Mean seasonal difference (SE) in maximum daily temperature between forest stand types and b: rate of increase in difference in maximum daily temperature between forest stand types (SE) per one degree increase in maximum daily ambient temperature.

	Regeneration-Hemlock		Regeneration-Deciduous		Deciduous-Hemlock	
Season	Mean (SE)	P-value	Mean (SE)	P-value	Mean (SE)	P-value
a.						
Spring	5.57 (0.48)	<0.001	5.05 (0.51)	<0.001	2.52 (0.44)	<0.001
Summer	5.81 (0.24)	<0.001	4.74 (0.25)	<0.001	1.08 (0.19)	<0.001
Fall	3.60 (0.36)	<0.001	2.65 (0.36)	<0.001	0.95 (0.32)	0.003
Winter	3.19 (0.26)	<0.001	1.43 (0.28)	<0.001	1.77 (0.26)	<0.001
b.						
Spring	0.28 (0.02)	<0.001	0.22 (0.02)	<0.001	0.08 (0.01)	<0.001
Summer	0.42 (0.03)	<0.001	0.36 (0.03)	<0.001	0.06 (0.01)	<0.001
Fall	0.17 (0.01)	<0.001	0.16 (0.01)	<0.001	-0.01 (0.01)	0.471
Winter	0.06 (0.01)	<0.001	0.02 (0.01)	0.028	0.04 (0.01)	<0.001

Table 1.5 Percent of moose GPS locations recorded when temperatures exceeded seasonal upper critical temperatures (increased metabolic rates, -5 and 14° C, and open mouthed panting, and 0 and 20° C, for winter and summer, respectively; Renecker and Hudson 1986).

	Spring			Summer			Fall		
	Day	Night	Season	Day	Night	Season	Day	Night	Season
Below 14◦C UCT	50.4	80.8	63.6	8.2	24.6	14.9	44.4	73.9	59.8
Above 14◦C UCT	49.6	19.2	36.4	91.8	75.4	85.1	55.6	26.1	40.2
Above 20◦C UCT	19.8	2.0	12.1	56.6	16.6	40.3	18.3	3.6	10.6

	Early winter			Late Winter		
	Day	Night	Season	Day	Night	Season
Below -5◦C UCT	15.1	24.0	20.7	24.3	42.7	34.6
Above -5◦C UCT	84.9	76.0	79.3	75.7	57.3	65.4
Above 0◦C UCT	57.7	41.5	31.7	48.1	28.5	37.2

Table 1.6 Comparison of the magnitude of change in proportional use of thermal shelters and open habitats across temperature classes during summer from recently published articles on moose habitat use-temperature interactions. Proportional use values were estimated from Fig. 3 of van Beest et al. 2012 and Fig. 1 of Dussault et al. 2004. Temperature classes for Dussault et al. 2004 represent the coldest 20th percentile, the middle 20th percentile, and warmest 20th percentile of ambient temperatures.

Authors	Location	Vegetation Cover	Temperature Classification and Proportion of Use			Change in use
van Beest et al. 2012	Norway		$<14^o$ C	$\geq 14^oC$ and $< 20^oC$	$\geq 20^oC$	
	Telemark	Mature Conifer	0.42	0.52	0.57	+ 0.15
		Young Spruce	0.39	0.29	0.25	- 0.14
	Hedmark	Mature Conifer	0.57	0.61	0.6	+ 0.03
		Young Spruce	0.05	0.05	0.04	- 0.01
Broders et al. 2012	Nova Scotia		10^oC - 16^oC		20^oC - 26^oC	
		Softwood	0.4		0.48	+ 0.08
		Mixwood	0.3		0.26	- 0.04
		Open	0.2		0.15	- 0.05
		Water	0.06		0.07	+ 0.01
Dussault et al. 2004	Quebec		< 20th percentile	40-60th percentile	80-100th percentile	

			<14° C	≥14°C and <20°C	≥20°C	
		Mature Conifer	0.23	0.3	0.35	+ 0.12
Wattles and DeStefano	Massachusetts					
		Conifer and Wooded Wetlands	0.19	0.28	0.43	+ 0.24
		Regeneration	0.64	0.49	0.36	- 0.28

Figures

Figure 1.1 Study area location in west-central Massachusetts and bordering areas of adjacent Vermont and New Hampshire; state borders marked with heavy solid lines, central and western portions of the study areas depicted with dashed lines, and major roadways shown with fine solid lines. Higher elevation depicted with darker colors. Location of study area in northeastern United States in inset map.
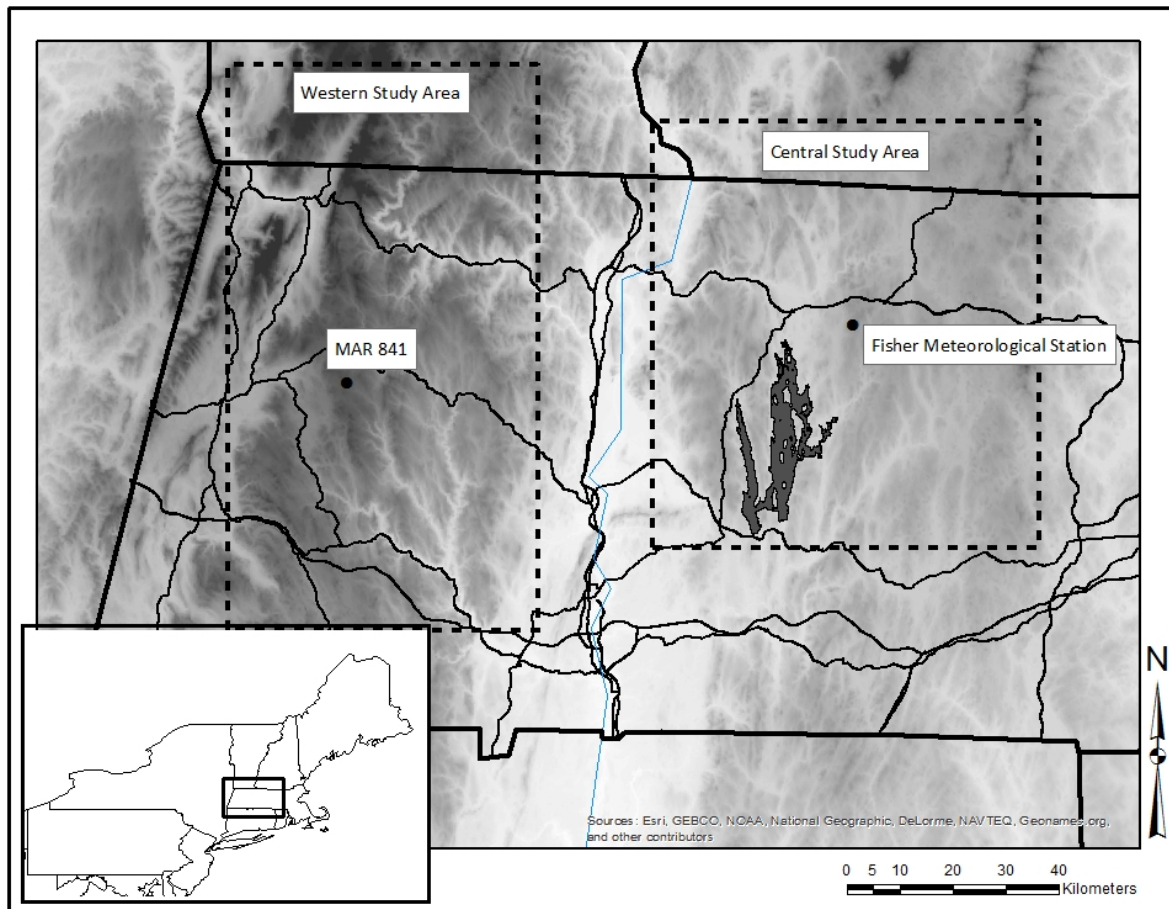
Figure 1.2 Mean daily minimum and maximum temperatures (2002-2008) in central Massachusetts relative to upper critical temperatures for moose (increased metabolic rates, -5 and 14° C, and open mouthed panting, and 0 and 20° C, for winter and summer, respectively; Renecker and Hudson 1986). Upper critical temperatures (UCT) for spring and fall are represented with dashed line due to the uncertainty of the appropriate UCT during these seasons.
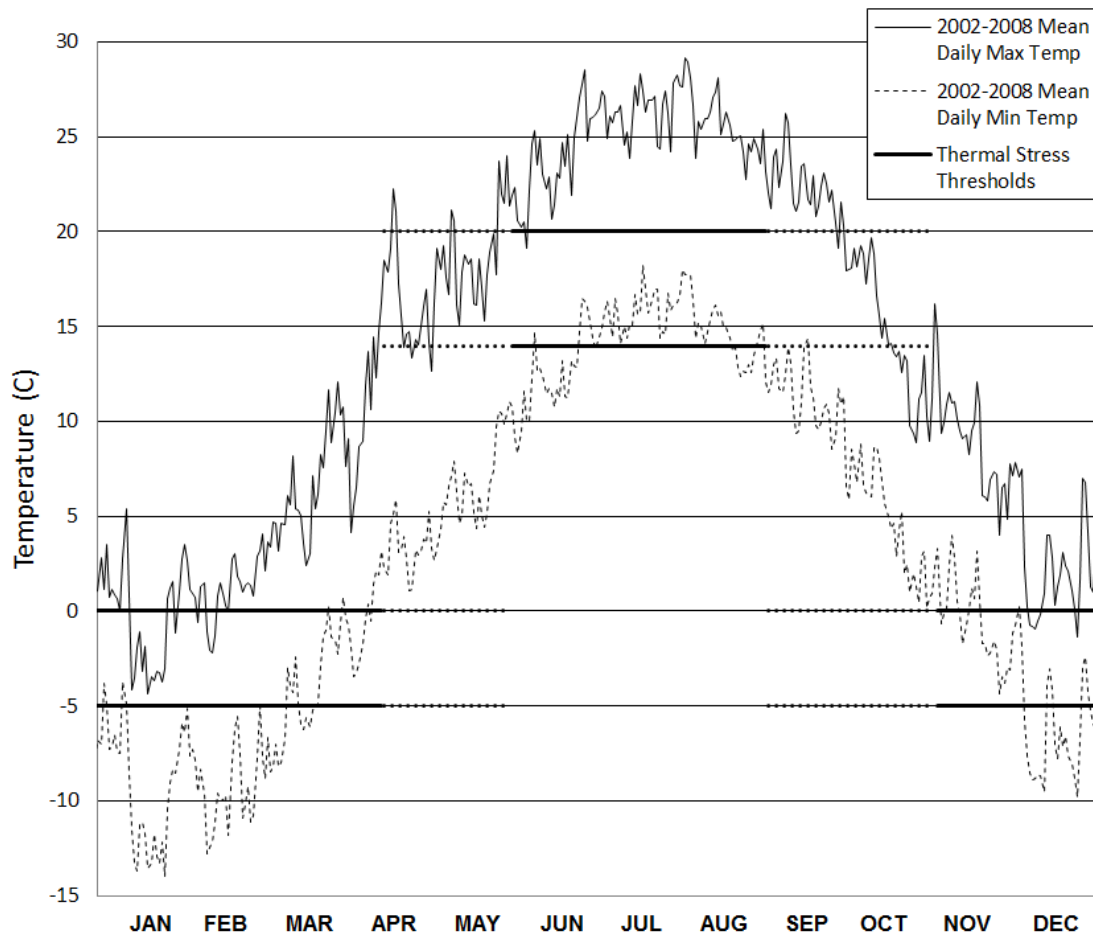
Figure 1.3 Mean daily maximum temperatures recorded by ibuttons temperature sensors in regenerating (circles and top line), mature deciduous (+ and middle line), and mature hemlock (triangles and bottom line) stands relative to daily maximum ambient temperature for spring, summer, fall, and winter.
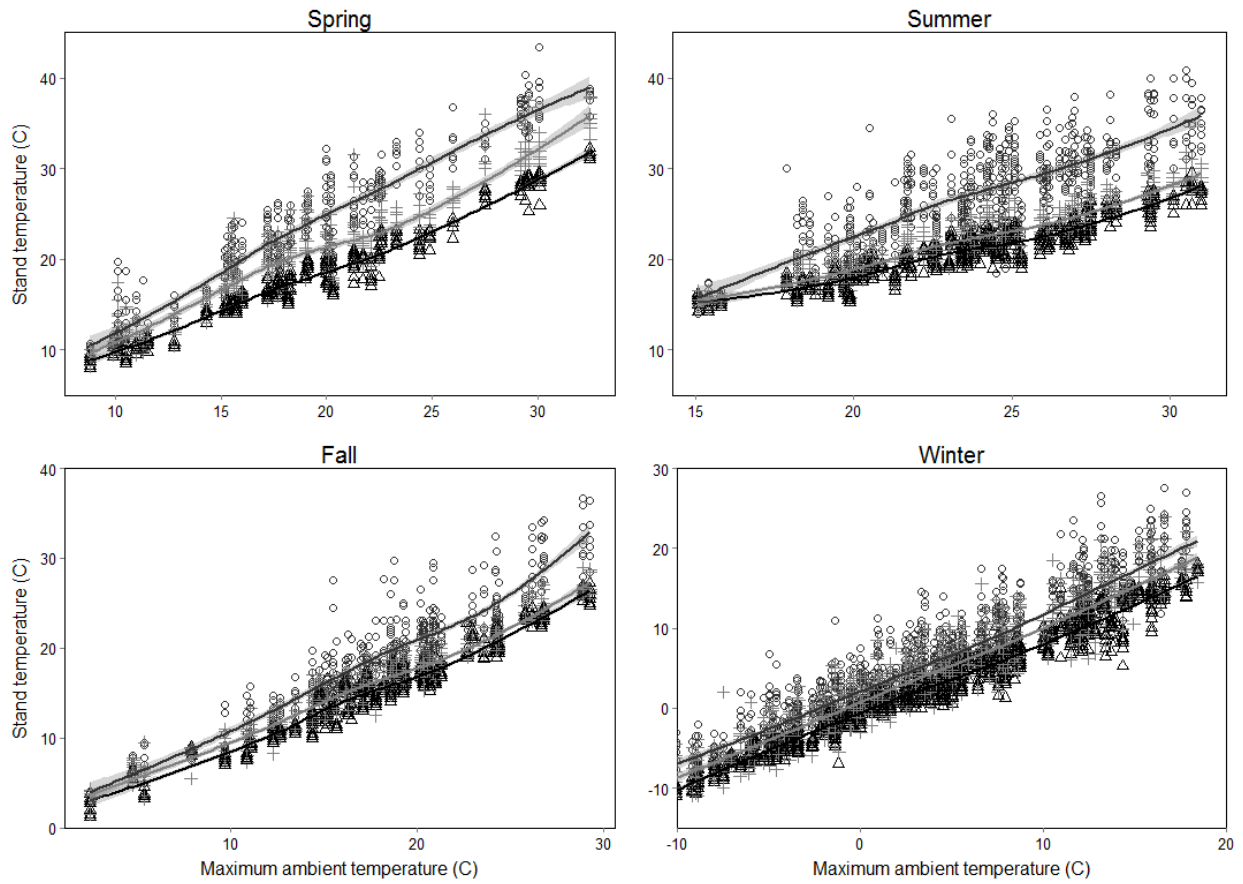
Figure 1.4 The proportional use of cover types with 95% confidence intervals versus temperature class and time of day in central Massachusetts during spring, summer, and fall. 'A' denotes use significantly different than hot, 'B' use significantly different than warm, and 'C' daytime use significantly different than night. Definition of cover types; Regenerating forests (Regen), Deciduous forest (Decid), Coniferous forest (Con), Mixed coniferous and deciduous forest (Mixed), Forested wetlands (WWet), and Open wetlands (OWet).
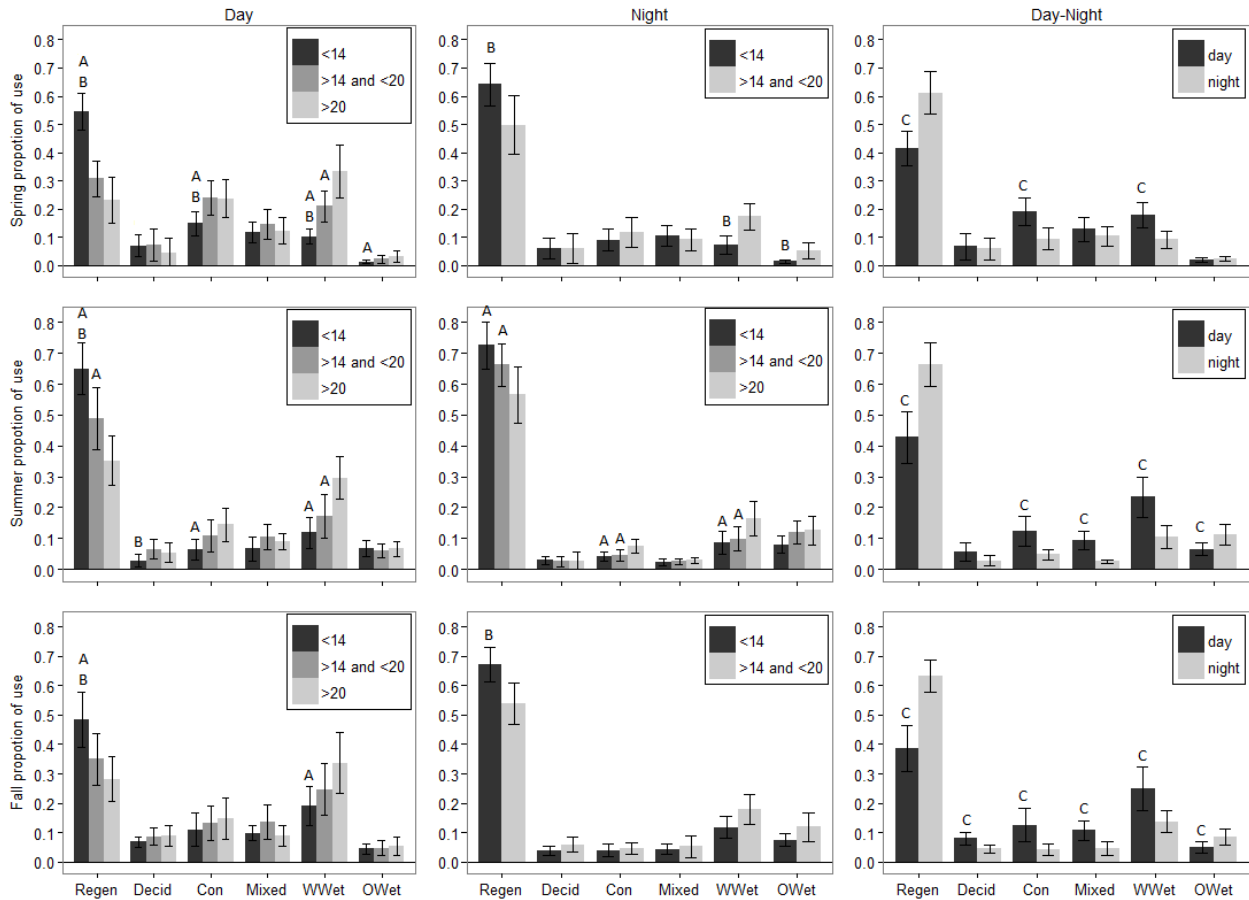
Figure 1.5 The proportional use of cover types with 95% confidence intervals versus temperature class and time of day in western Massachusetts during spring, summer, and fall. 'A' denotes use significantly different than hot, 'B' use significantly different than warm, and 'C' daytime use significantly different than night. Definition of cover types; Regenerating forests (Regen), Deciduous forest (Decid), Coniferous forest (Con), Mixed coniferous and deciduous forest (Mixed), Forested wetlands (WWet), and Open wetlands (OWet).
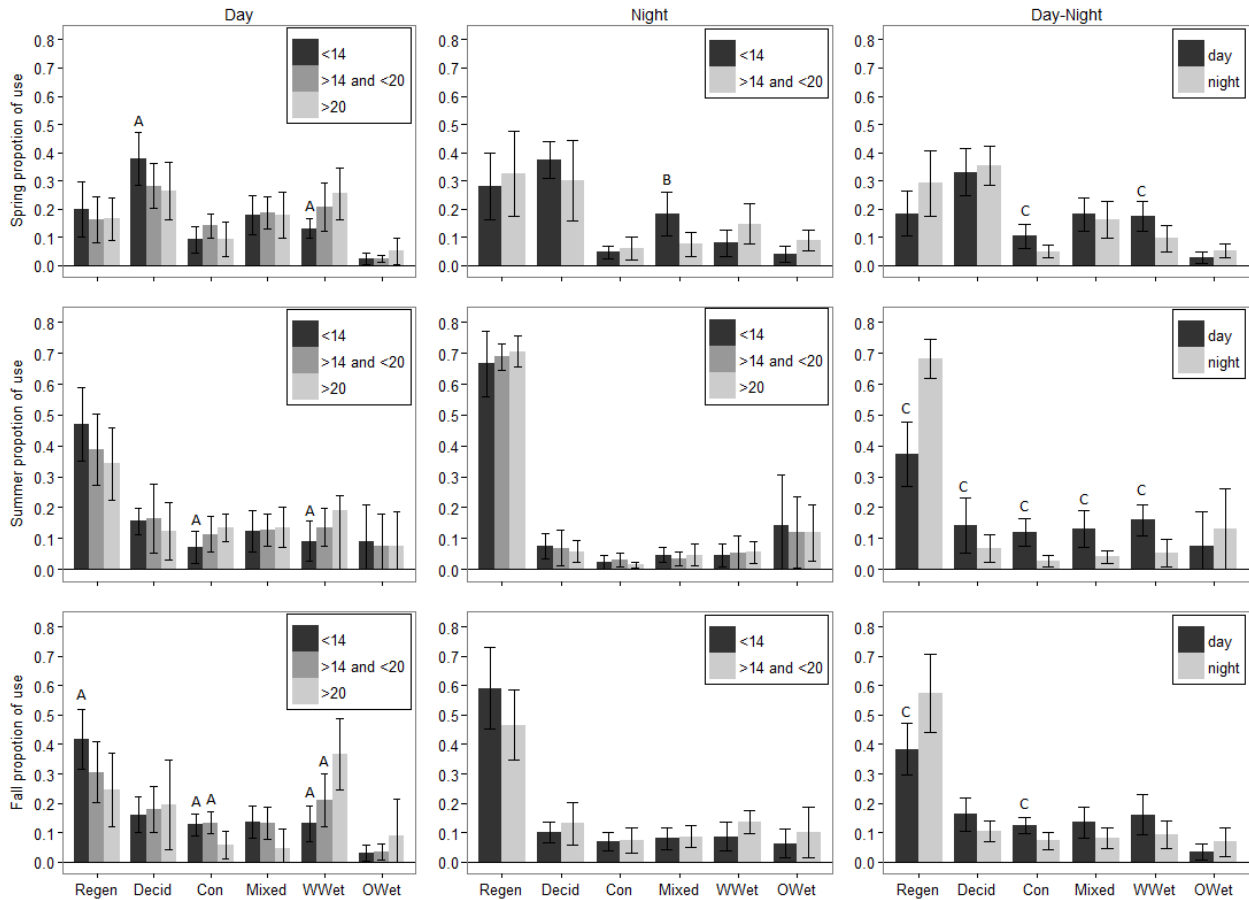
Figure 1.6 The proportional use of cover types with 95% confidence intervals versus temperature class and time of day in central Massachusetts during early and late winter. 'A' denotes use significantly different than hot, 'B' use significantly different than warm, , 'C' use significantly different than very hot, and 'D' daytime use significantly different than night. Definition of cover types; Regenerating forests (Regen), Deciduous forest (Decid), Coniferous forest (Con), Mixed coniferous and deciduous forest (Mixed), Forested wetlands (WWet), and Open wetlands (OWet).
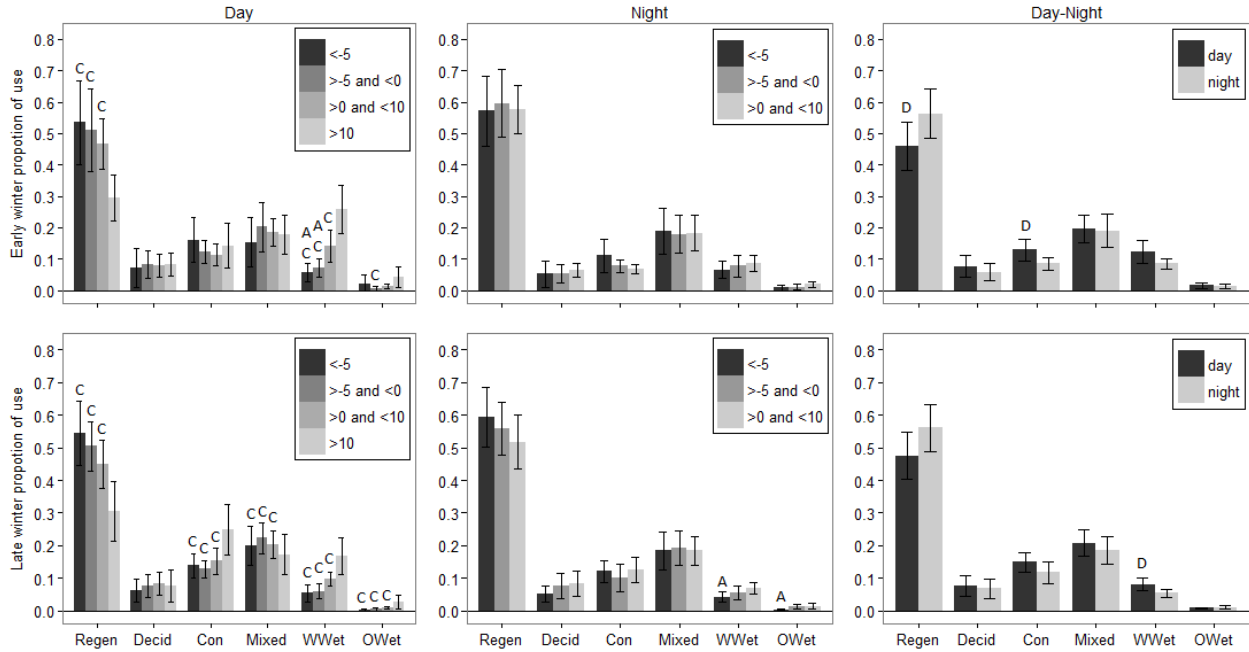
Figure 1.7 The proportional use of cover types with 95% confidence intervals versus temperature class and time of day in western Massachusetts during early and late winter. 'A' denotes use significantly different than hot, 'B' use significantly different than warm, 'C' use significantly different than very hot, and 'D' daytime use significantly different than night. Definition of cover types; Regenerating forests (Regen), Deciduous forest (Decid), Coniferous forest (Con), Mixed coniferous and deciduous forest (Mixed), Forested wetlands (WWet), and Open wetlands (OWet).
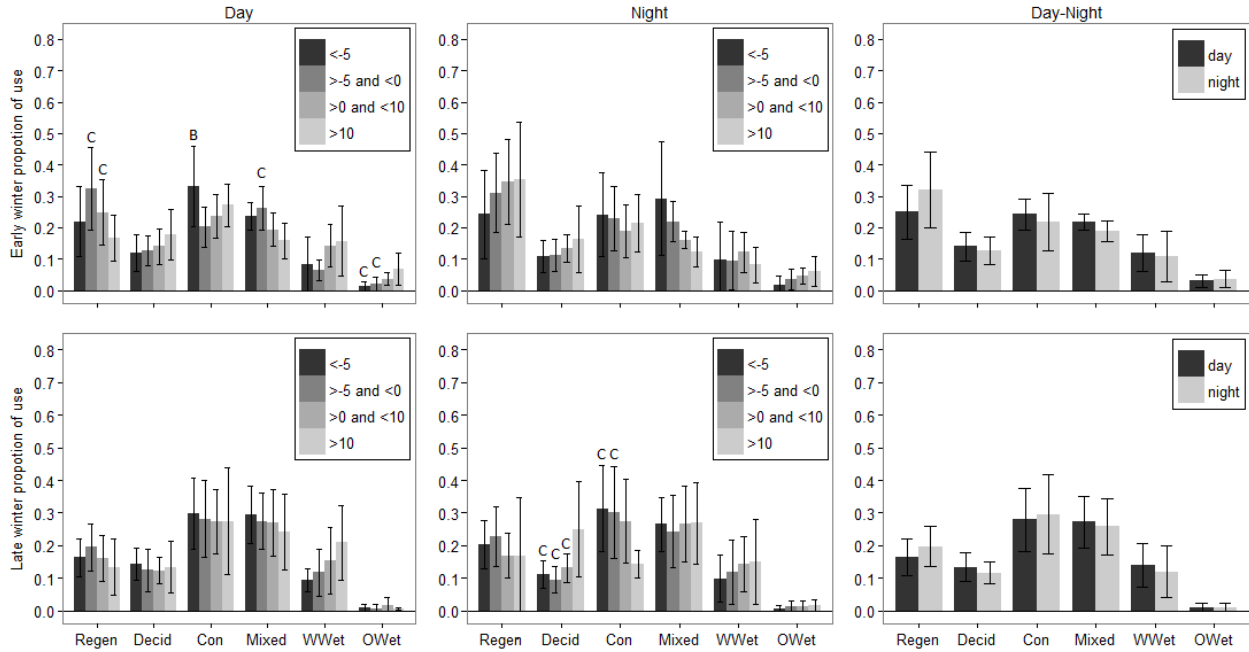
Figure 1.8 Seasonal hourly proportional use of vegetation cover types with 95% confidence intervals in central Massachusetts, scale for regeneration is 0-0.8, for all other cover types it is 0-0.4.

Spring
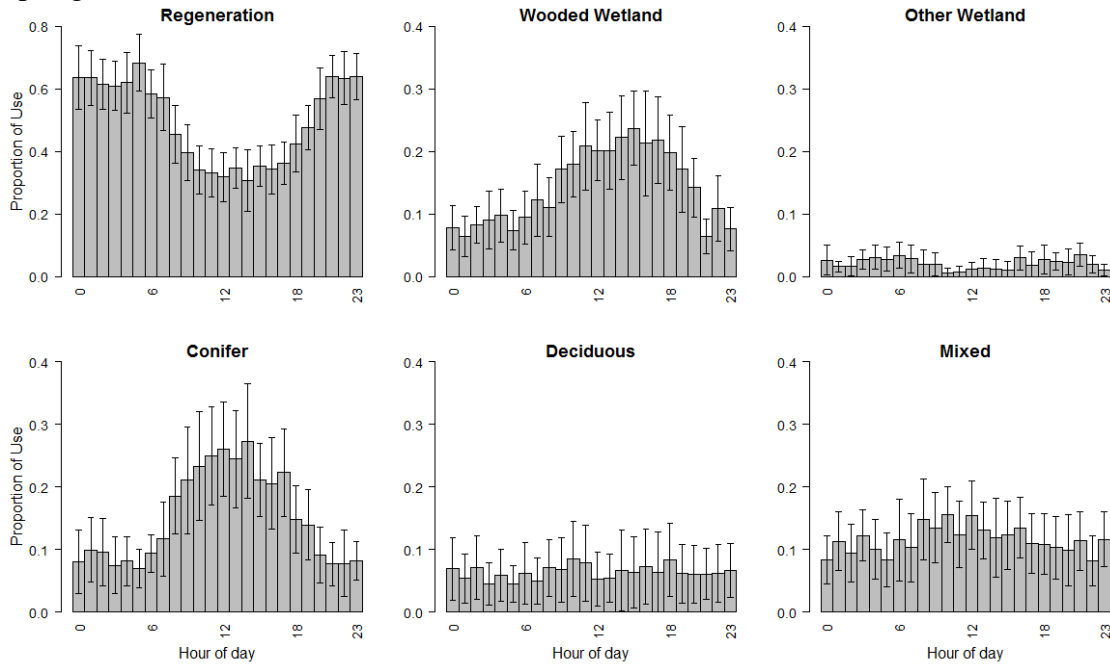
Summer
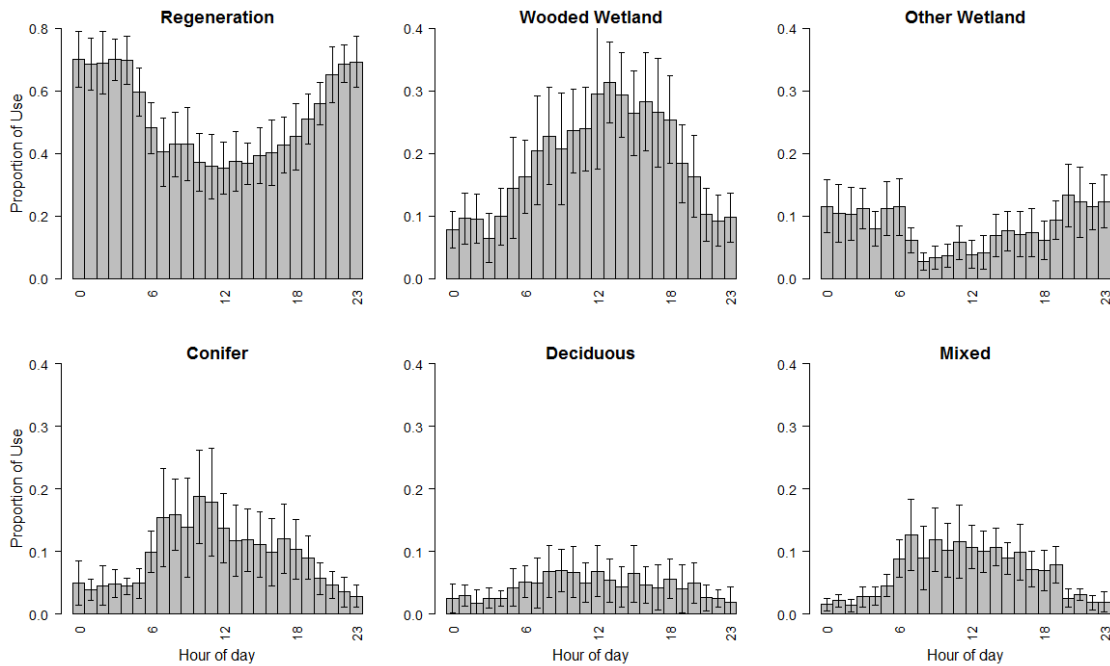
Fall
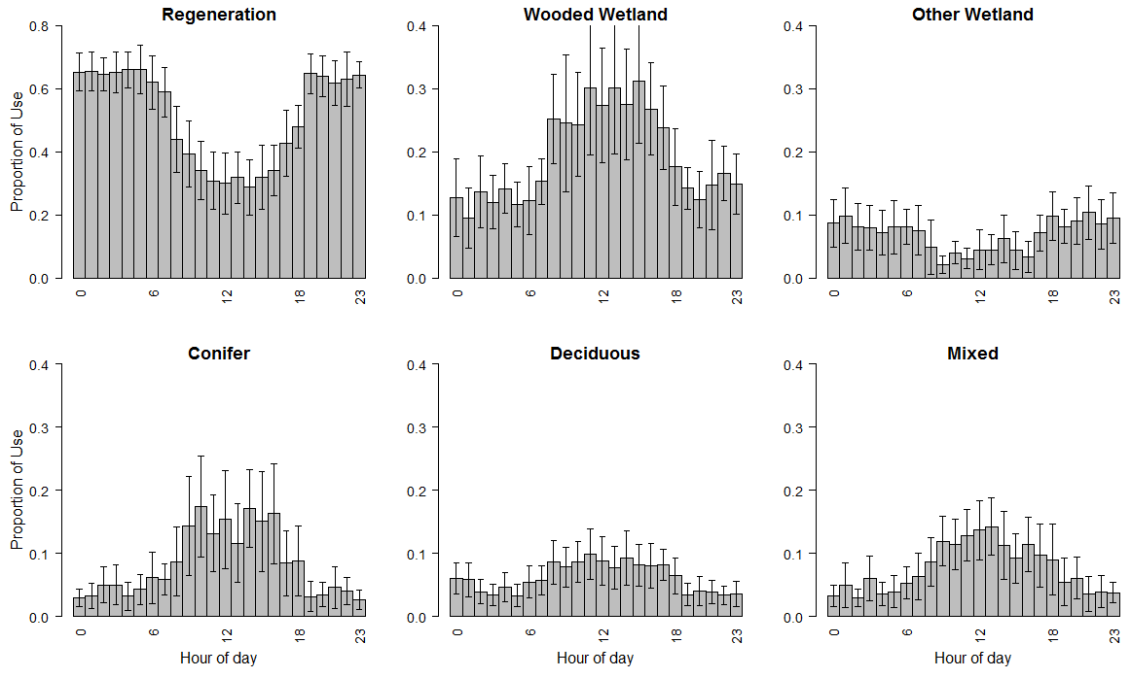
Early winter
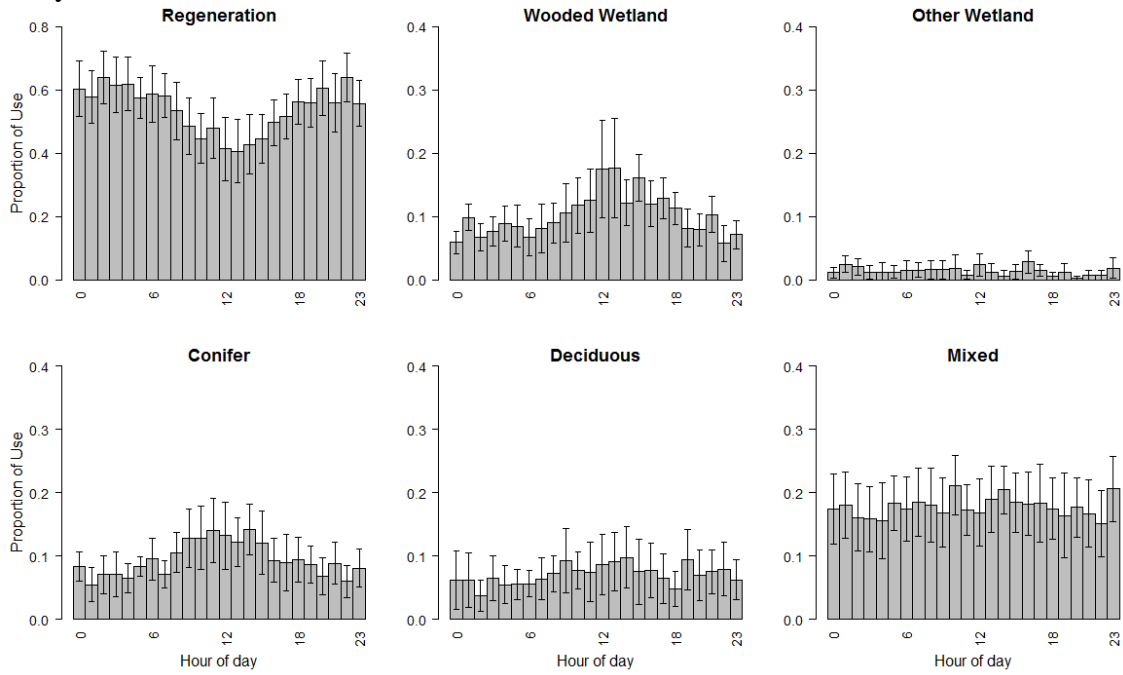
Late winter
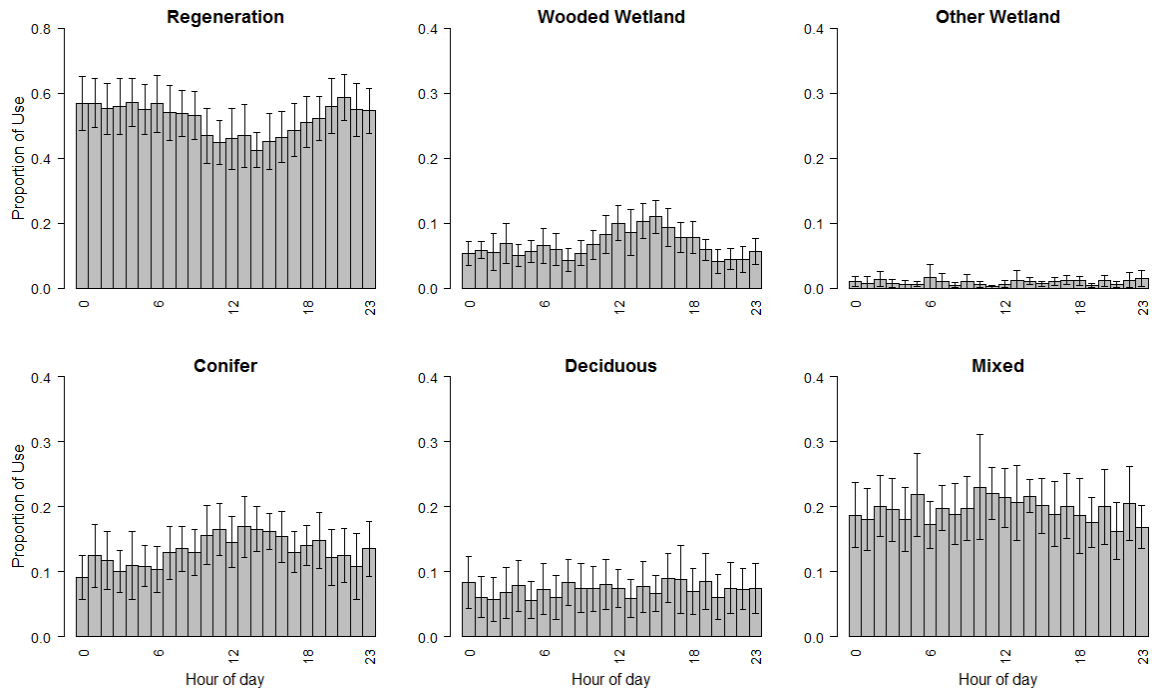
Figure 1.9 Seasonal hourly proportional use of vegetation cover types with 95% confidence intervals in western Massachusetts. Note scale for regeneration is 0-0.8 and 0-0.4 for all other cover types; except for deciduous in spring, which is also 0-0.8.
Spring
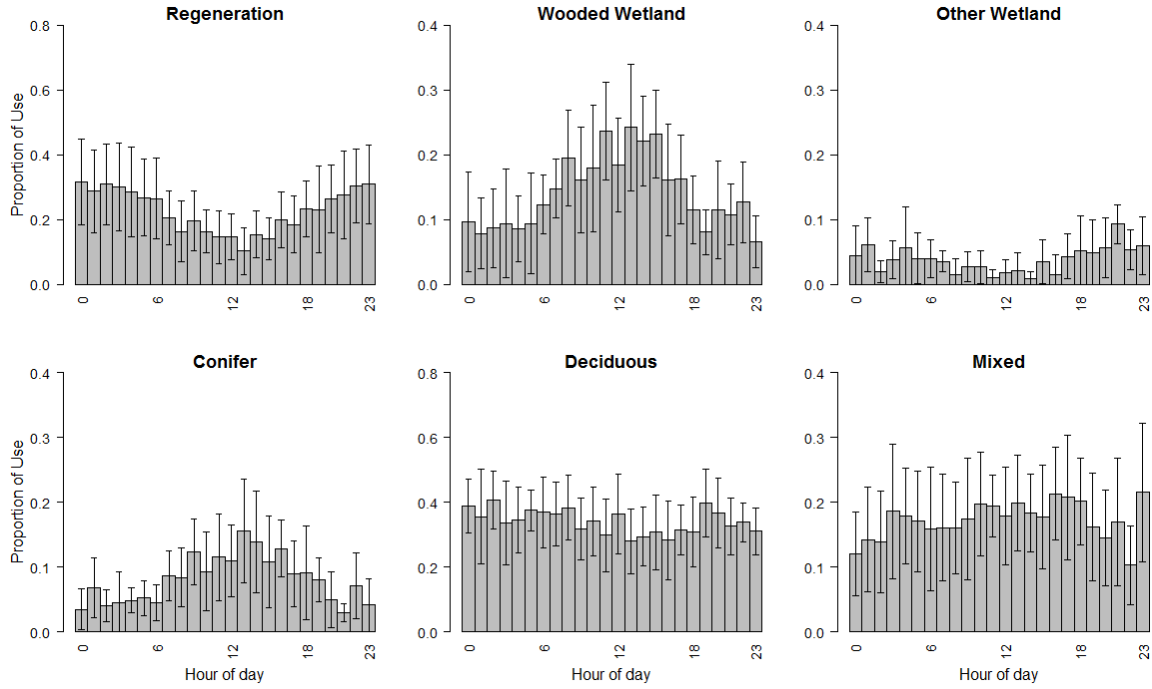
Summer
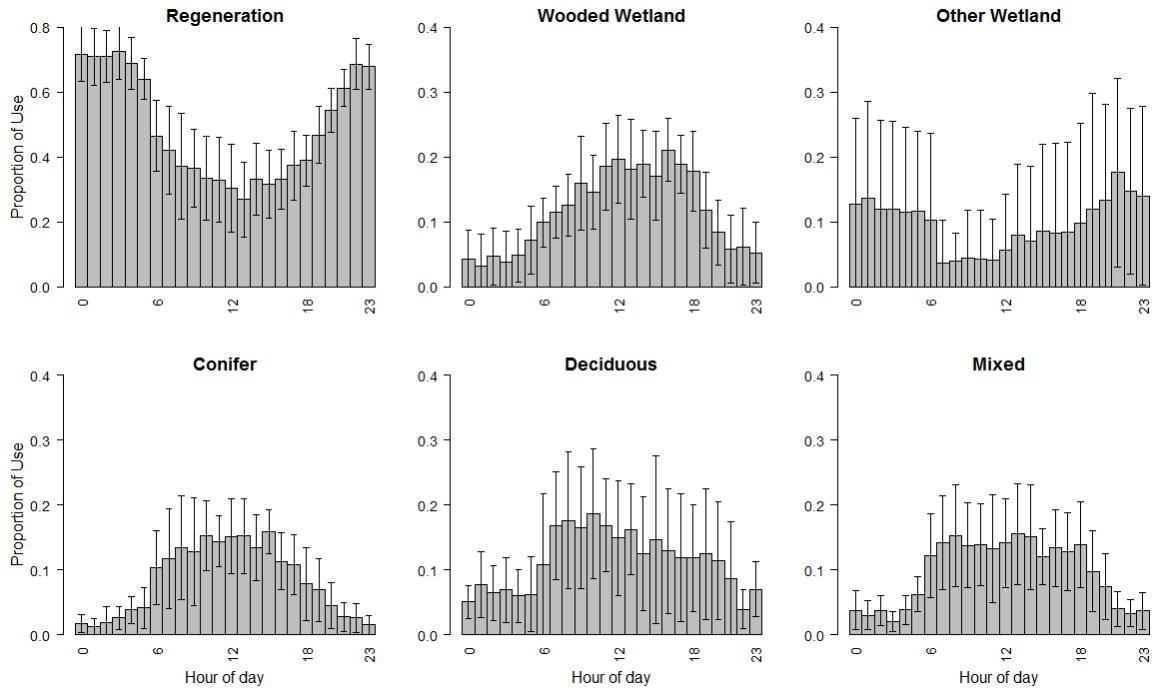
Fall
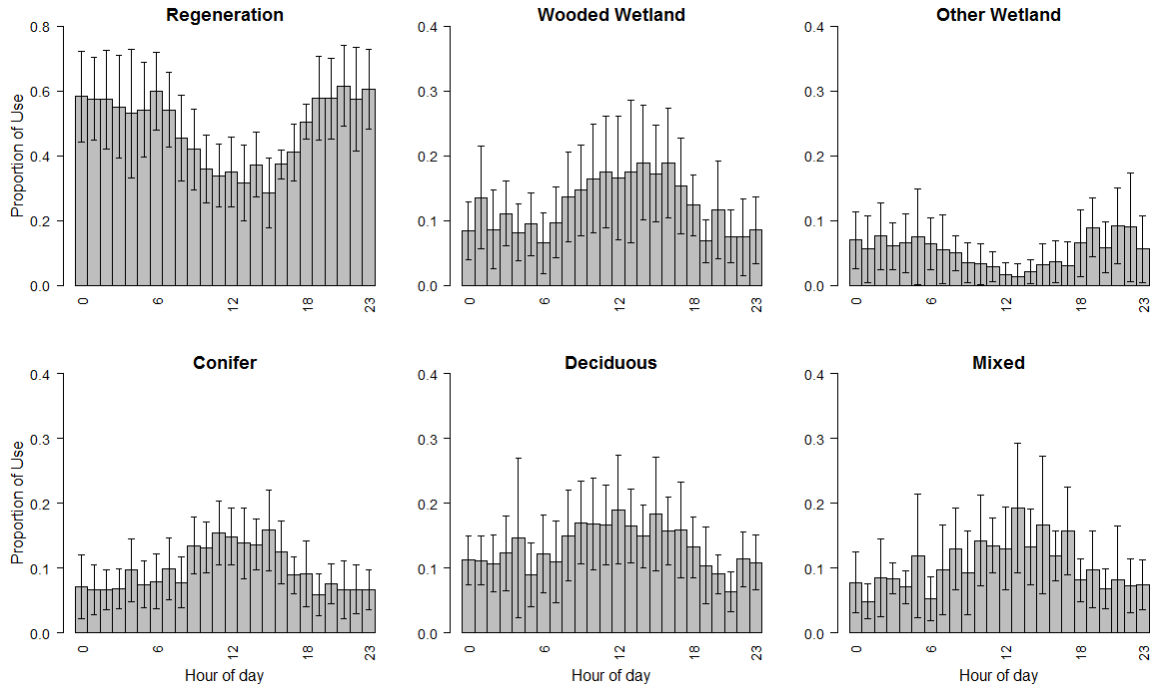
Early winter
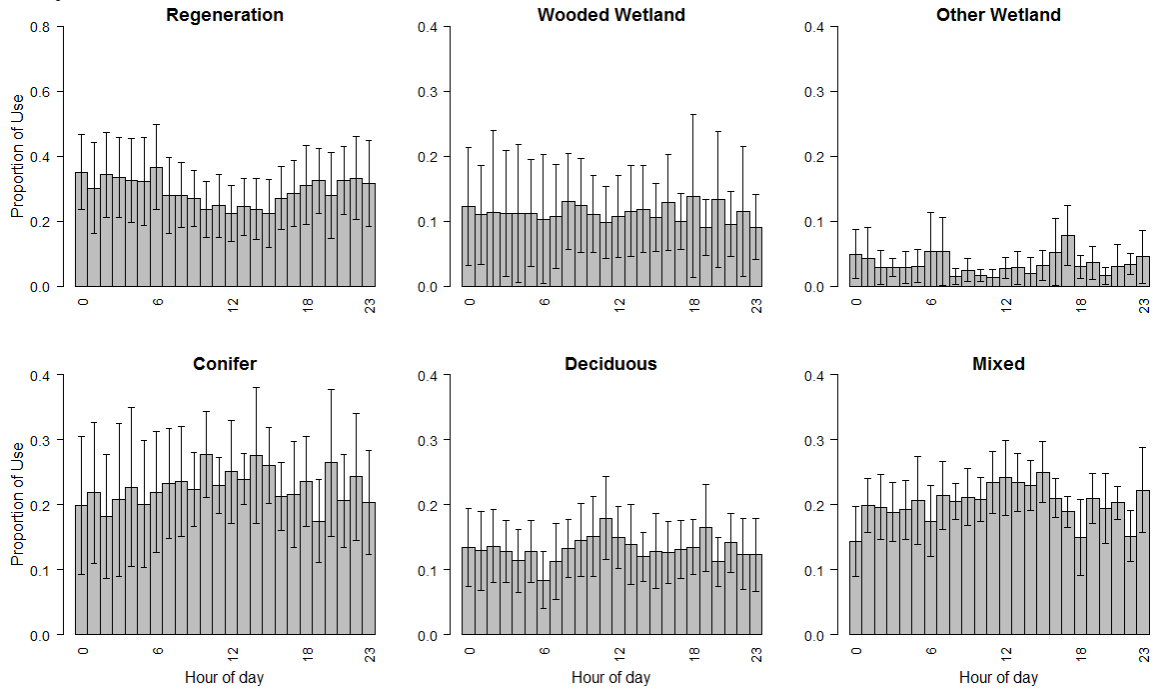
Late winter
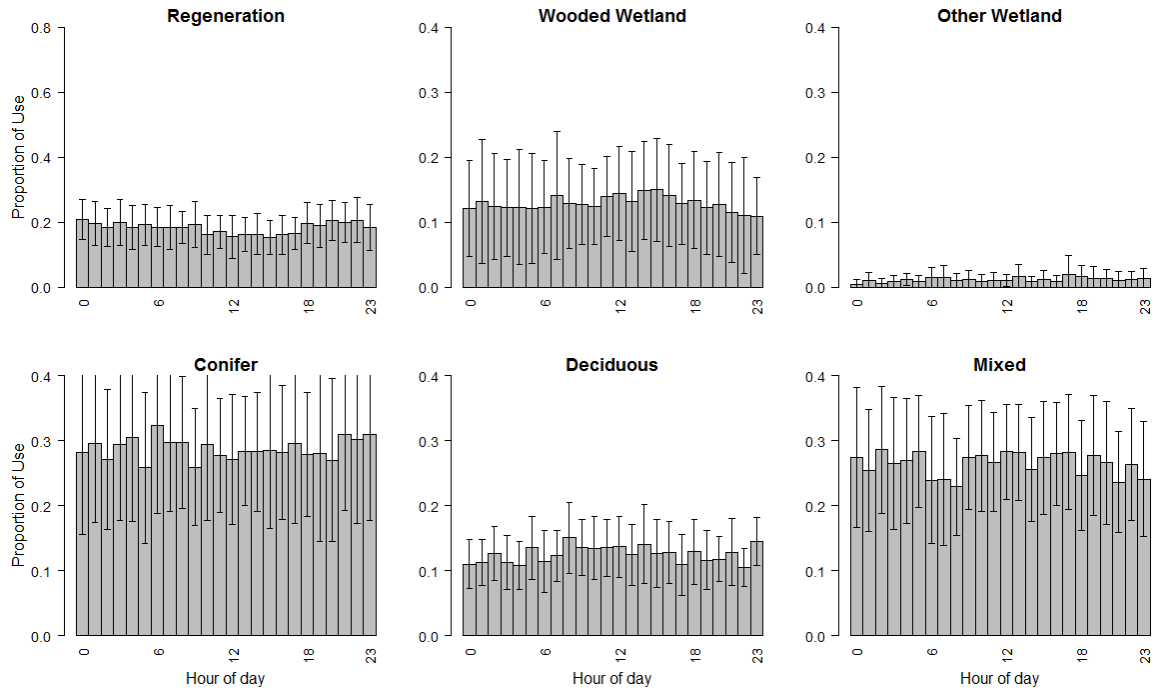
Figure 1.10 Seasonal hourly mean movements (m) with 95 % confidence intervals in central (top) and western (bottom) Massachusetts.
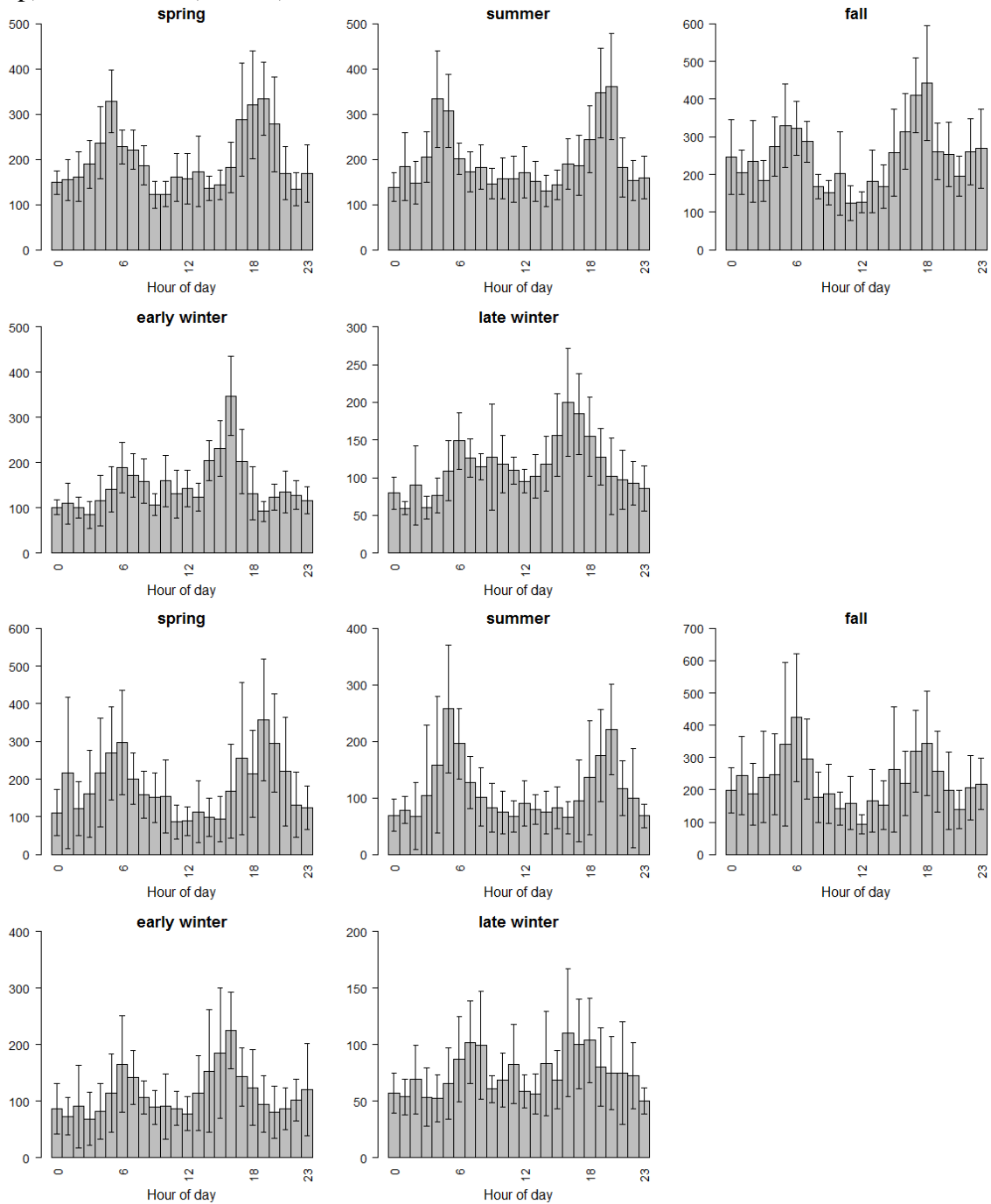
Figure 1.11 The relative probability of selection of cover types versus ambient temperature for day and night, and mean selection ratios of cover types with 95% confidence intervals for day and night in central Massachusetts during spring, summer, and fall. For relative probability of selection the magnitude of the y-scale is meaningless, but allows for the comparison of selection between cover types within any one season and photo-period. Note ambient temperature scale differs among seasons and photo-period. For day-night selection ratios 'A' signifies significant difference in selection between day and night. Definition of cover types; Regenerating forests (Reg), Deciduous forest (Dec), Coniferous forest (Con), Mixed coniferous and deciduous forest (Mix), Forested wetlands (WWet), and Open wetlands (OWet).

Figure 1.12 The relative probability of selection of cover types versus ambient temperature for day and night, and mean selection ratios of cover types with 95% confidence intervals for day and night in western Massachusetts during spring, summer, and fall. For relative probability of selection the magnitude of the y-scale is meaningless, but allows the for comparison of selection between cover types within any one season and photo-period. Note ambient temperature scale differs among seasons and photo-period. For day-night selection ratios 'A' signifies significant difference in selection between day and night. Definition of cover types; Regenerating forests (Reg), Deciduous forest (Dec), Coniferous forest (Con), Mixed coniferous and deciduous forest (Mix), Forested wetlands (WWet), and Open wetlands (OWet).
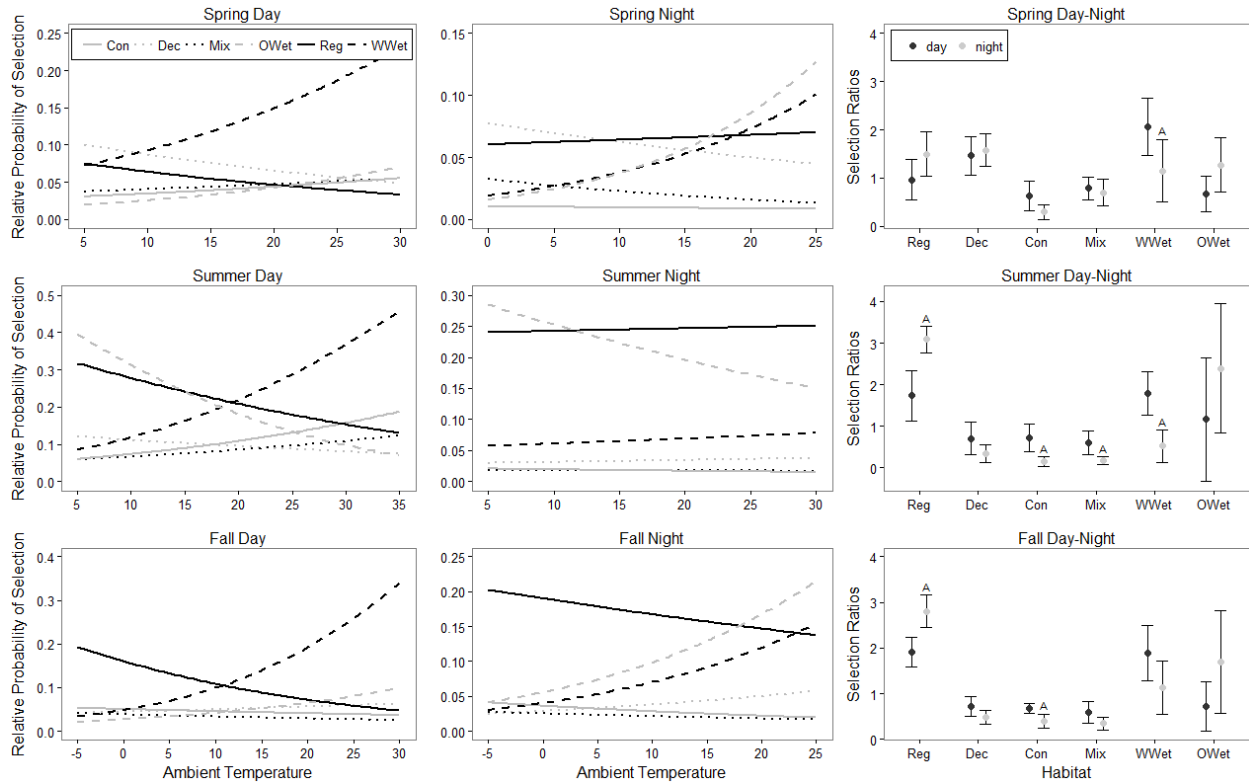
Figure 1.13 The relative probability of selection of cover types versus ambient temperature for day and night, and mean selection ratios of cover types with 95% confidence intervals for day and night in central Massachusetts during early and late winter. For relative probability of selection the magnitude of the y-scale is meaningless, but allows for the comparison of selection between cover types within any one season and photo-period. Note ambient temperature scale differs among seasons and photo-period. For day-night selection ratios 'A' signifies significant difference in selection between day and night. Definition of cover types; Regenerating forests (Reg), Deciduous forest (Dec), Coniferous forest (Con), Mixed coniferous and deciduous forest (Mix), Forested wetlands (WWet), and Open wetlands (OWet).

Figure 1.14 The relative probability of selection of cover types versus ambient temperature for day and night, and mean selection ratios of cover types with 95% confidence intervals for day and night in central Massachusetts during early and late winter. For relative probability of selection the magnitude of the y-scale is meaningless, but allows for the comparison of selection between cover types within any one season and photo-period. Note ambient temperature scale differs among seasons and photo-period. For day-night selection ratios 'A' signifies significant difference in selection between day and night. Definition of cover types; Regenerating forests (Reg), Deciduous forest (Dec), Coniferous forest (Con), Mixed coniferous and deciduous forest (Mix), Forested wetlands (WWet), and Open wetlands (OWet).

CHAPTER 2

MOOSE-VEHICLE COLLISIONS IN MASSACHUSETTS: DISPROPORTIONATE RISK IN A HUMAN-DOMINATED LANDSCAPE

2.1 Abstract

Massachusetts is one of the most densely populated states in the United States and has an extremely dense road network that receives very high traffic volumes. Roads and road networks have many negative impacts on wildlife population, one of the main effects being direct mortality associated with vehicle collisions. Moose-vehicle collisions (MVCs) occur throughout the geographic range of moose where roads bisect moose habitat. I analyzed the database of moose-vehicle collisions reported to the Massachusetts Division of Fisheries and Wildlife to assess the risk of MVCs in this human-dominated landscape and to determine if there were any landscape features or features of the road network that increase the probability of MVCs. Moose-vehicle collisions were a considerable source of additive mortality for the state moose population, with an estimated 3-5% of the population involved in a MVC each year. This was one of the highest rates of moose-vehicle collisions relative to the size of the moose population reported in the literature. The human fatality rate resulting from the MVCs is the highest reported anywhere, with 1 out of every 140 MVCs resulting in a human fatality. The majority (86%) of MVCs occurred on interstate and state highways, which were roads with high speed limits and high traffic volumes. Moose-vehicle collisions occurred on these roads at much higher rates than would be predicted based on their availability on the landscape and were much more likely to occur where major roads bisected relatively ecologically intact portions of the landscape.

2.2 Introduction

The natural reoccupation of the northeastern United States by moose (*Alces alces*) is an excellent example of how successful population and habitat management helped to restore a species that was essentially eliminated from a large portion of its historic range (Alexander 1993, Bontaites and Gustafson 1993, Wattles and DeStefano 2011). However, this conservation success story has resulted in a potentially dangerous situation with a large and wide-ranging animal now living in a landscape that became human dominated in its absence (Wattles and DeStefano 2013b).

Moose-vehicle collisions (MVCs) are common wherever moose and vehicle traffic co-exist (Table 2.1). States, provinces, and countries with large, high-density moose populations almost invariably have high frequencies of moose-vehicle collisions, including the northeastern United States (Danks and Porter 2010, Wattles and DeStefano 2011). In the northeastern United States >1,000 MVCs and between 2 and 8 human fatalities resulting from those collisions occurred annually from 1998 to 2007 (Wattles and DeStefano 2011).

While the moose population in Massachusetts is relatively low, the human population and levels of human development are extremely high. As a result, as the moose population grew rapidly in the 1990s, the number of MVCs correspondingly increased (Fig. 2.1, Wattles and DeStefano 2011). As moose move about their large home ranges (mean home ranges 62, 89, and 176 km^2 for mature females, males, and immature males, respectively) (Wattles and DeStefano 2013b), they invariably encounter, interact with, and cross roads of various types, traffic volumes, and speed limits. With each crossing, moose and unsuspecting drivers are at risk of a potentially fatal collision.

Due to their large body size, long legs, and high center of gravity, vehicle collisions with moose often result in the vehicle taking the legs out from under the moose and the body of the moose colliding with the windshield and passenger compartment. These devastating collisions often lead to the death of the moose, extreme damage to the vehicle, and driver and passenger injury or even death. High speeds and traffic volumes increase the risk and severity of these collisions (Lavsund and Sandegren 1991, Belant 1995, Joyce and Mahoney 2001, Seiler 2005, Danks and Porter 2010, Rolandsen et al. 2011, Neumann et al. 2012).

Moose-vehicle collisions and vehicle collisions with other large wildlife have been studied extensively and many factors have been shown to contribute to the likelihood of collisions, including roadway configuration, traffic volumes, speed limits, time of day, season, habitat associations, and topography (Joyce and Mahoney 2001, Dussault et al. 2006, Danks and Porter 2010). Our objectives were to examine the record of 424 MVCs reported to the Massachusetts Division of Fisheries & Wildlife (MassWildlife) from 1980 to 2012, determine the factors that contribute to those collisions, and see how these patterns in a highly developed landscape compared to other portions of moose range.

2.3 Study Area

Our study area was located in western two-thirds of Massachusetts, USA (Fig. 2.1). The area was bounded on the east by Interstate (I-) 495 from the New Hampshire border to its intersection with I-290, then by I-290 between I-495 and I-90, by I-90 between I-290 and I-84, and by I- 84 south of I-90 to the Connecticut border. This area encompassed all reported MVCs of known location in Massachusetts, with the exception of 8 that occurred on Interstate highways in the greater Boston metropolitan area.

The study area is composed of six ecoregions that differ in the frequency of MVCs as well as several factors that likely influence the distribution of MVCs, including the amount and quality of forest habitat (Hall et al. 2002), moose density (Massachusetts Division of Fisheries and Wildlife, unpublished data), topography, and levels of human development, road density, and traffic volumes (Hall et al. 2002). The 6 ecoregions are the Southern New England Coastal Plain (CP), the Worcester Plateau (WP), the Connecticut River Valley (CTRV), the Berkshire Plateau (BP), the Western New England Marble Valleys, and the Taconic Mountains. Due to the limited number of MVCs in the Taconic Mountains ($n = 4$) and the Western New England Marble Valleys ($n = 7$), we combined those two ecoregions with the BP and the CTRV, respectively (ecoregions of similar characteristics), and hereafter refer to the combined regions as the Berkshire Plateau and the Connecticut River Valley.

Massachusetts has by one of the lowest densities of moose reported in the literature, about 0.14 moose/km^2 (MassWildlife, unpublished data; Van Ballenberghe and Ballard 2007), and one of the highest densities of humans, human development, and road densities in the United States (5th most densely populated state with 324 people/km^2 statewide) (DeStefano et al. 2005, U. S. Census Bureau 2010, Fig. 2.3 and 2.4). However, neither humans nor moose occur evenly on the landscape. The majority of moose in that state occur in the Worcester Plateau and Berkshire Plateau ecoregions (Massachusetts Division of Fisheries and Wildlife, unpublished data). These two ecoregions have greater amounts of forested habitat (Hall et al. 2002), higher elevation and more varied topography (Fig. 2.2), and lower human populations (Fig. 2.3), and correspondingly lower levels of human development, road density, and traffic volume (Figs. 2.4, Table 2.2), than the Connecticut River Valley and Coastal Plain.

2.4 Methods

2.4.1 Moose-Vehicle Collisions and Large Animal Response Team Data

We obtained records of MVCs reported to the Massachusetts Division of Fisheries and Wildlife and the Massachusetts Environmental Police from 1980 to 2012. The records contained information on the date, town, roadway, sex and age of the animal, and other data pertaining to the MVCs. The spatial accuracy and other details of the reports were variable. We screened the reports to remove duplicate and questionable reports and separated the reports into "known" and "unknown" location reports. Known locations reports were those that at a minimum had information on the town and roadway where the MVCs occurred. Unknown reports typically only had information on the town where the MVC occurred and were not used in the analysis. Using the known records, we created a GIS layer that mapped the location of the MVCs. Many of the known locations had further detail on the specific MVC location (e.g., at an intersection, near an exit ramp or mile marker, or near a business or other identifiable feature) that allowed for reasonably accurate mapping of the location. Other known location reports only contained information on the town and roadway. For these reports, we randomly located the MVC along the length of the roadway in that town. To represent the available roads in the study area we generated 2,000 random locations along the road network. We measured all the variables for the random locations in the same manner as we did for the MVC locations. We performed all GIS work in ArcGIS 10.1 (Environmental Systems Research Institute, Inc. 2011).

We also obtained records of Large Animal Response Team (LART) events related to moose in Massachusetts. The LART is composed of Massachusetts Division of Fisheries and Wildlife and Massachusetts Environmental Police personnel that respond when moose wander into highly developed areas and pose a risk to public health and safety or the safety of the

animal. LART responses to these situations range from doing nothing to hazing the animal out of the area, tranquilizing and relocating the animal, or euthanizing the animal. We compiled and mapped all LART responses that resulted in the moose being relocated or euthanized.

2.4.2 Moose-Vehicle Collision Modeling

2.4.2.1 Model Structure

We used Program R version 3.0.1 for all statistical analyses (R Development Core Team 2005). We modeled the patterns in MVCs using the R package lme4 (Bates et al. 2012). We used logistic regression in a use:availability framework (Manly et al. 2002) and assumed the exponential form after Johnson et al. (2006). The relative probability of selection, or in this case occurrence of MVC $\hat{w}(x)$, is a function of the coefficients (β_i) of the model variables x_i, and was estimated using logistic regression (Manly et al. 2002) with the equation:

$$\hat{w}(x) = \exp[\beta_1 x_i + \beta_2\, x_i + \beta_3\, x_i]$$

Based on the obvious differences in moose density, topography, habitat integrity, and level of human development among ecoregions we modeled the patterns of MVCs separately for the four ecoregions: the Worcester Plateau, the Connecticut River Valleys, the Berkshire Hills, and the Coastal Plain.

2.4.2.2 Roadway and Landscape Covariates

To determine what factors influenced the likelihood of moose vehicle collisions we measured variables of the roadway and landscape around the MVC and random locations, including the road class, speed limit, traffic volume, topography, and several measures of habitat integrity (see Table 2.3 for variable description). Due to the limited number of MVCs on class 4 and 5 roads we combined class 3, 4, and 5 roads into a single category, hereafter referred to as

class 3 roads. We were unsure of the most appropriate scale to measure the habitat integrity

variables; therefore, we measured the variables connectivity, natural, and road density at scales

of 2.5, 5, 7.5, and 10 km out from the MVC and random locations and tested for the most

appropriate scale. In each ecoregion, we selected the most appropriate variable and scale of the

variable by comparing 12 identical saturated models, each containing one of the three habitat

integrity variables at one of the four scales. We used Akaike information criteria difference for

small sample sizes (AICcΔ) and Akaike weights (*w*) (Burnham and Anderson 2004), to identify

the best variable-scale combination, then used that variable-scale combination for the remainder

of the model selection procedure for that ecoregion.

2.4.2.3 Model Selection and Validation

We screened combinations of variables for high levels of correlation and limited

candidate models to those where all variables had a variance inflation factor (VIF) < 3 (Zuur et

al. 2010). This screening prevented using a combination of speed limit and average daily traffic

for models for the Coastal Plain; we therefore restricted model selection to models using road

class in that ecoregion. We used the variables relief and slope to describe topography around the

MVC; however, the two variables were highly correlated. Based on AICcΔ and *w*, slope was a

better predictor of MVC location than relief, and so we used slope as the topography variable in

model selection.

We started the model selection procedure with two saturated models, each containing

either class or both speed and average daily traffic (ADT) as roadway variables, plus slope and

the selected habitat integrity variable (e.g., natural at a scale of 10 km) as landscape variables,

and several interactions (e.g., class*natural10 or speed*ADT, speed*natural10, and

ADT*natural10). We then used a drop one procedure (Zuur et al. 2010) and AICcΔ, *w*, and

likelihood ratio tests to select the most parsimonious best fitting models (Burnham and Anderson 2004). If no single candidate model was clearly selected, based on AICcΔ and *w*, we used model averaging to estimate model coefficients and standard errors using full model averaging (Burnham and Anderson 2004, Symonds and Moussalli 2011). Model averaging was only required for models of the Coastal Plain.

Akaike information criteria can be used to select the best fitting and most parsimonious of the candidate models; however, it cannot be used to determine how well the models fit the data. We used k-fold cross-validation (Boyce et al. 2002) to evaluate model fit. This method uses subsets of the data, withholding 20% of the data to test models generated with the remaining 80%, and then generates Spearman's rank correlation coefficients (r_s) with high r_s indicative of good model fit.

2.5 Results

2.5.1 Annual and Monthly Patterns of MVCs

From 1980 to 2012, 424 moose-vehicle collisions were reported to the Massachusetts Division of Fisheries & Wildlife (Fig. 2.1). Between 30 and 50 MVCs have been reported annually since 2003, with the exception of years when the state's Deer and Moose Project Leader position, the person responsible for recording reports of MVCs, was vacant or recently filled (2007-2009 and 2011). There have been 3 MVCs that resulted in a human fatality, one each in 2003, 2007, and 2012; a rate of 1 human fatality for every 140 MVCs or 0.7% of reported MVCs. During this time, 78.9 % of known location and 77.2% of unknown location MVCs resulted in the animal dying or being euthanized due to its injuries. The status of the moose from the remaining collisions was reported as unknown, left the scene, or injured. Moose-vehicle

collisions were most frequent in May ($n = 75$), with the frequency in June ($n = 48$) and July ($n = 47$) remaining high, and a secondary peak observed in September and October ($n = 48$ and 57, respectively) (Fig. 2.5).

2.5.2 Location of MVC and LART Responses

Moose-vehicle collisions were most likely to occur in the Worcester Plateau, with 56% of known and 51% of unknown location MVCs, respectively (Table 2.4). The Berkshire Plateau, Connecticut River Valley, and Coastal Plain had 19, 11, and 14% of known location MVCs and 21, 16, and 12% of unknown location MVCs, respectively. Large Animal Response Team events were far more common in the more heavily developed CP (20 relocations [R] and 19 euthanizations [E]) and CRTV (33 R and 3 E) than in the WP (8 R and 4 E) or the BP (5 R and 0 E). An additional 6 relocations and 10 euthanizations occurred in the Coastal Plain outside our study area in the greater Boston metropolitan area. Large Animal Response Team responses most commonly occurred in urban centers and to a much lesser extent on major roadways (Fig. 2.6).

In the Worcester and Berkshire Plateaus, MVCs were most common on state highways (class 2 roads), accounting for 61.8 and 62.5% of MVCs, respectively (Table 2.4), followed by interstate highways (class 1 roads) with 29.0 and 20.3% of MVCs, respectively. In the Connecticut River Valley and Coastal Plain class 1 roads were the most likely location for MVCs (45.9 and 48.9%, respectively), followed by class 2 roads (35.1 and 28.9%, respectively). Of the 3 human fatalities resulting from MVCs, 2 occurred on class 1 roads and the third on a class 2 road; all three occurred in the WP. Throughout the study area, MVCs occurred on class 1 and 2 roads at a rate that was highly disproportionate to the availability of those roads types on the landscape (Table 2.5). The likelihood of MVCs occurring on major local arteries was much lower (3.2-11.1% of MVCs) and occurred in proportion to the availability of these roads, with

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the exception of in the WP. Moose-vehicle collisions were far less likely on the original class 4 and 5 roads and occurred at a rate far below the availability of these roads on the landscape.

2.5.3 Model Selection and Fit

2.5.3.1 Worcester Plateau

Road class was a much better predictor of MVC location than average daily traffic, speed limit, or both in the Worcester Plateau (AICcΔ = 42.6 between the final model and the best model with speed limit and ADT; Table 2.6 and 2.7). The proportion of natural habitat at a scale of 5 km around collision and random locations was the best habitat integrity variable in the WP; the probability of MVCs increased with increasing proportion of natural habitat. There was an interaction between road class and natural in the WP, and the influence of natural on the probability of MVCs occurrence was greatest on class 2 roads. The relative probability of occurrence of MVCs increased rapidly on class 2 roads with increasing proportion of natural habitat, especially across the range of natural from 0.7 to 0.9 (Fig. 2.7). The relative probability of MVCs occurring on class 1 roads was high across the range of natural occurring in the WP, and increased at a low rate with increasing proportion of natural habitat. The relative probability of MVCs on class 3 roads was low across the range of natural, but increased slightly above a proportion of natural of 0.9. The relatively probability of MVCs on class 1 roads was many times greater than class 2 or 3 roads at low levels of natural and remained many times greater than class 3 roads across the range of natural. However, the difference in probability of MVCs on class 1 and 2 roads decreased rapidly at levels of natural above 0.7, and eventually the probability was greater on class 2 roads at the highest levels of natural. The relative probability of a MVC decreased by a factor of 0.84 for each 1-degree increase in slope.

2.5.3.2 Connecticut River Valley

Models for the Connecticut River Valley that contained speed limit and average daily traffic were better predictors of MVC location than those with road class (AICc△ = 3.8 between the final model and the best model with class) (Table 2.6 and 2.7). Connectivity at a scale of 7.5 km was the best habitat integrity variable in predicting MVCs. There was a strong positive relationship between the relative probability of a MVC and both speed limit and ADT. The relative probability of a MVC increased by a factor of 1.55 for every 10 kph increase in speed limit and increased rapidly with increasing ADT, beginning at an ADT of about 10,000 vehicles per day. An interaction between ADT and connectivity resulted in a higher rate of increase in the probability of MVCs with increasing ADT at higher levels of landscape connectivity (Fig 2.8). The relative probability of a MVC decreased by a factor of 0.84 for each 1-degree increase in slope.

2.5.3.3 Berkshire Plateau

Models for the Connecticut River Valley that contained speed limit and average daily traffic were better predictors of MVC location than those with road class (AICc△ = 6.6 between the final model and the best model with class) (Table 2.6 and 2.7). The proportion of natural habitat at a scale of 10 km was the best habitat integrity variable in the BP. The final model for the BP included interactions between both speed limit and ADT, and ADT and natural. The multiple interactions make determining the influence of any individual variable or interaction difficult. However, it is clear that the relative probability of a MVC increased with increasing speed limit and that the probability increased rapidly with increasing ADT from <1,000 to 5,000 vehicles per day (Fig 2.9). It also appears that for any speed limit-ADT combination, the relative probability increases with increasing proportion of natural habitat. Discerning this pattern in

made more difficult by the influence of slope, which decreased the probability of a MVC by a factor of 0.92 for every 1-degree increase.

2.5.3.4 Coastal Plain

Models for the Coastal Plain that contained speed limit and average daily traffic were better predictors of MVC location than those with road class (AICcΔ = 1.9 between the final model and best model with class) (Table 2.6 and 2.7). However, a high correlation between speed limit and ADT (VIF > 3.0) prevented those variables being included in the same model; therefore, road class was used in models for the CP. Class was the dominant variable in predicting MVCs in the CP. The relative probability of a MVC occurring on a class 1 or 2 road was 74.8 and 12.4 times greater than on a class 3 road. Connectivity at a scale of 10 km out from MVC and random locations was the best habitat integrity variable in predicting MVCs and increased the probability of a MVC by a factor of 1.69 for a 0.1 increase in connectivity. Slope had a minimal effect on MVC location; a 1-degree increase in slope decreased the relative probability of a MVC by a factor of 0.98 in the CP.

2.5.3.5 Model Validation

Model fit was reasonable for all models; r_s of 0.77 (0.51 – 0.97), 0.79 (0.51 – 0.97), 0.83 (0.76-0.87), and 0.60 (0.31-0.94) for the Worcester Plateau, Connecticut River Valley, Berkshire Hills, and Coastal Plain, respectively.

2.6 Discussion

2.6.1 Relative Risk

The absolute number of reported MVCs in Massachusetts is relatively low, as would be expected with a low-density moose population. However, the risk of a moose being involved in a MVC relative to the size of the population (3-5% of the estimated population) is as high as or higher than elsewhere in moose range (Table 2.1). Massachusetts also has the highest rate of human fatality resulting from MVCs (0.7%) reported anywhere (Table 2.1). The large proportion of moose in the population involved in MVCs and the heightened risk of human deaths can be attributed to the human-dominated landscape of Massachusetts, particularly the high density of very high traffic volume and high-speed roads that bisect the landscape. High speed limit (Lavsund and Sandegren 1991, Joyce and Mahoney 2001, Seiler 2005, Danks and Porter 2010, Neumann et al. 2012) and high traffic volume (Belant 1995, Joyce and Mahoney 2001, Seiler 2005, Danks and Porter 2010, Rolandsen et al. 2011) are widely reported to increase the likelihood and severity of MVCs.

2.6.2 MVC Location and Modeling

Moose-vehicle collisions were most common in the two blocks of more contiguous moose habitat in Massachusetts where moose density was greatest, the Worcester Plateau and the Berkshire Plateau, with the WP containing over half of reported MVCs in the state. The far greater frequency of MVCs in the WP than the BP reflected the gradient of increasing human development, road density, and traffic volume west-to-east, as one gets closer to the greater Worcester and Boston metropolitan areas. Within the WP, moose-vehicle collisions were more frequent in the eastern portion of the ecoregion in the towns with higher human population

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density and traffic volume. The frequency of moose-vehicle collisions in the CTRV and CP, despite the scarcity of resident moose in those ecoregions, suggests how inhospitable those environments are to moose because of the high levels of human development. Moose-vehicle collisions in these ecoregions would be even more frequent if not for the number of moose removed from problem animal situations by the LART.

In all ecoregions, the vast majority of MVCs occurred on the high speed limit and high traffic volume class 1 and 2 roads. Occurrence ratios for class 1 roads (proportion of total MVCs:proportion of road density) were very high relative to all other road types, even class 2 roads. Traffic volumes on class 1 roads in Massachusetts were extremely high, with mean average daily traffic of 23,000-79,000 vehicles per day depending on the ecoregion (Table 2.2). Additionally, traffic on class 1 roads traveled at very high speeds. Posted speed limits were 89 to 105 km_*h^{-1} (kph) but traffic typically moved at speeds of 105 to 130 kph. The combination of the high vehicle volume and extreme speed means that moose have very little chance of successfully crossing these roads when they encounter them. As a result, in the WP and BP, MVCs are common where these roads bisect the ecoregions, despite class 1 roads being very limited. The greater frequency and odds that MVCs occurred on class 1 roads in the CTRV and CP was likely due to the even greater traffic volumes in those ecoregions -- 2-4 times the ADT on class 1 roads than in the WP and BP (Table 2.2). The odds of MVCs on class 2 roads were still very high compared to lower classes of roads, and MVCs were actually more frequent on class 2 than class 1 roads in the WP and BP due to their greater density in those ecoregions. The traffic volumes on class 2 roads in Massachusetts were still very high and were comparable to the upper end of the range of ADT reported in other regions and that represented the greatest risk of MVCs (Seiler 2005, Danks and Porter 2010).

Not surprisingly, either road class or the combination of traffic volume and speed limit were the driving variables in models predicting MVCs in all ecoregions. The risk of MVC occurrence increased rapidly with increasing speed limit and average daily traffic (or on class 1 and 2 roads). Similarly, human fatalities resulting from MVC occurred on high-speed roads.

Danks and Porter (2010) reported that the odds of a MVC in Maine increased 35% for every 8 kph increase in speed limit, and the probability of MVC increased sharply at speeds above 70 kph. Seiler (2005) reported that 57% of MVCs in Sweden occurred on roads with speed limits of 90 kph and that 65 and 83% of human fatalities in Sweden occurred on those roads in his model and test areas, respectively. Joyce and Mahoney (2001) reported that the risk of severe injury was 2 times greater at highway (80 to 100 kph) compared to non-highway speeds in Newfoundland. Lavsund and Sandegren (1991) reported 3 times the likelihood of severe injuries in collisions at 70 to 90 kph compared to lower speeds in Sweden. Seventy three percent of known location MVCs in Massachusetts occurred on high-speed roads ($n = 43$, 136, and 63 for posted or estimated speed limits of 72, 80-89, and 105 kph, respectively). The posted speed limits for the roads where the 3 human fatalities occurred in Massachusetts were 89, 89, and 105 kph.

Similarly, Joyce and Mahoney (2001) showed nearly a doubling of the risk of MVCs at high compared to low traffic volumes regardless of moose density. Danks and Porter (2010) determined that the odds of MVC increased 57% for each 500 vehicle/day increase in traffic volume. Dussault et al. (2006) reported a 42% increase in MVCs on Fridays when traffic was highest. Neumann et al. (2012) reported that 64% of all MVCs occurred on major roads; however, major roads were only 29% of all roads.

Both Seiler (2005) and Danks and Porter (2010) reported a humped pattern in the probability of MVCs compared to average daily traffic in Sweden and Maine, respectively. That is, probability increased with increasing ADT, peaking at 5,000 and between 2,500 and 6,000 vehicles per day (vpd) in Sweden and Maine, respectively, before decreasing to near zero probability at 8,000 to 10,000 and 12,500 vpd. Seiler (2005) suggested that roads of the highest traffic volumes were repellents to wildlife and actually reduced the likelihood of collisions. Seiler (2005) also proposed that roads with traffics volumes of 1,000 to 10,000 vpd would result in considerable mortality, but that ADT >10,000 vpd would be insurmountable barriers. The traffic volumes at the peaks suggested by these authors correspond with the mean ADT on class 2 roads in Massachusetts. Traffic volumes on class 1 roads in Massachusetts far exceeded the upper limits suggested to be complete barriers to movement and repellants to wildlife.

The high risk of MVCs on class 1 roads does suggest that they serve as barriers to movement and that moose that attempt to cross them have a high probability of being involved in a collision. If higher traffic volume roads did not repel moose as Seiler (2005) suggested, the number of attempted crossings would not be limited, and the already high occurrence ratios on these roads would be even higher. Data from our collared moose suggests that moose cross class 3, 4, and 5 roads at a much greater frequency than class 2 roads and that moose may avoid higher speed and traffic volume roads (USGS Massachusetts Cooperative Fish & Wildlife Research Unit [MACFRU], unpublished data). The high frequency of MVC one class 1 and 2 roads despite reduced crossing frequencies on these roads reinforces the risk of MVCs when moose do attempt to cross them.

2.6.3 Habitat Integrity

Increasing habitat integrity amplified the probability of moose-vehicle collisions in all ecoregions. Moose-vehicle collisions were clustered where high speed and high traffic volume roads bisected or ran adjacent to blocks of more intact moose habitat; i.e., where there was a greater probability moose would encounter the roads. This is similar to the pattern reported by Mountarkis and Gunson (2009) in Vermont, where MVCs were clustered on state highways where they intersected good moose habitat.

The interaction between habitat integrity and road class or traffic volume in the models revealed a thresholds of habitat integrity and traffic volume where the risk of MVC increased dramatically. Traffic volumes equivalent to those on state highways (class 2 roads) caused a rapid increase in the probability of moose-vehicle collisions. In the WP where class 2 roads passed through areas of >70% forested and wetland habitat, the probability of a MVC increased at a very high rate. In a similar way, higher levels of connectivity in the CTRV increased the probability of MVCs for a fixed level of ADT. In the uplands of the WP and BP, road shoulders along class 2 roads are very narrow and forested habitat verges along the edge of the pavement. This condition means that moose have to be practically in the roadway before they can be seen by drivers. Combined with the typically winding nature of class 2 roads in these areas and the speeds traveled on them, reaction time for drivers to avoid a collision is limited.

2.6.4 Seasonal Patterns

The seasonal patterns in MVCs differ between southern and northern portions of the species geographic range. In the southern range (e.g., Minnesota, Newfoundland, Quebec, Vermont), MVCs peak from May to July with a lesser peak during September and October (Belant 1995, Lavsund and Sandegren 1991, Groot Bruinderink and Hazebroek 1996, Joyce and

Mahoney 2001, Dussault et al. 2006, Montrakis and Gunson 2009, Danks and Porter 2010).

However, northern portions of moose range (e.g., Alaska, Sweden, British Columbia) have their

greatest occurrence of MVCs in winter due to deep snow and limited daylight hours (Child et al.

1991, Del Frate and Spraker 1991, Lavsund and Sandegren 1991, Garrett and Conway 1999, see

also Dussault et al. 2006 and references there-in). The seasonal patterns of MVCs we observed in

Massachusetts were very similar to the pattern reported for most southern portions of moose

range.

Dussault et al. (2006: 422) stated that, "Peak accident rates are usually associated with

major activity periods of cervids fulfilling particular requirements such as feeding, reproduction,

seasonal migration or even dispersal of juveniles.". The pattern we observed closely matched the

seasonal movement patterns of moose in Massachusetts (Wattles and DeStefano 2013b). The

peak in MVCs in May that continues through July parallels the relative peak in daily movement

rates at the end May and early June observed in both males and females, which corresponded to

the peak of vegetation quantity and quality. Additionally, calves of the year are dispersing at this

time of year, resulting naïve animals moving about the landscape. The secondary peak in

September and October corresponded with the large peak in daily movements for males

associated with the rutting period. The low rate of MVCs during the winter months agreed with

the low observed daily movement rates at that time of year (Wattles and DeStefano 2013b).

2.6.5 Mortality

Mortality related to moose-vehicle collisions likely has a considerable influence on

moose population dynamics in Massachusetts. Nearly 80% of reported MVCs resulted in the

direct death of the moose. Given the high speeds at which MVCs typically occurred, it is likely

that a large portion of the MVCs that resulted in an "injured" moose, or moose that "left the

scene", also eventually resulted in death. We observed a GPS-collared female that had greatly

reduced movement rates and injuries consistent with road rash after crossing a state highway; she

survived for several months before dying from her injuries. If we consider the suspected

considerable under-reporting of MVCs, it could be estimated >5% of the population in

Massachusetts is killed each year as a result of vehicle accidents. That is far greater than reported

elsewhere, with 1.2 – 1.8 % reported for Norway, Sweden, and Finland (Groot Bruinderink and

Hazebroek 1996), 0.6% in Newfoundland (Joyce and Mahoney 2001), 1% of the population and

19% of allowable harvest in Minnesota (Belant 1995), and <1% of the population but up to 10%

of allowable harvest in British Columbia (Child et al. 1991).

2.6.6 Mitigation

Large Animal Response Team activities related to moose in urban areas and on high-

speed roads is the primary form of mitigation of MVCs currently in use in Massachusetts. Team

responses occurred at much higher frequency in the more heavily developed CTRV and CP

ecoregions and were located primarily in urban centers. As such, LART responses likely do

reduce the number of MVCs in these areas; without them, the frequency of MVCs in the CTRV

and CP would be much higher. However, LART responses were rare in the WP and BP and had

almost no effect on MVCs along the state highway network in these ecoregions.

Fencing of roadways has been reported to be a highly effective means of limiting MVCs

and vehicle collisions with other wildlife (Lavsund and Sandgren 1991, McDonald 1991,

Clevenger et al. 2001, Leblond et al. 2006), with 70-95% and 80% reductions in MVCs along

fenced sections of road reported in Alaska and Sweden, respectively (Lavsund and Sandgren

1991, McDonald 1991). Approximately 20-30 years ago, all interstate highways in

Massachusetts were fenced with 2-meter chain-link fencing along the edge of the right-of-way

away from the road (Tim Dexter, Massachusetts Department of Transportation, personal communication). The fencing has not been maintained and is often in forested areas. As a result, there are likely breaks and downed fencing resulting from tree-fall and other factors. Despite this, fencing along the interstate highway system has likely prevented some moose from getting onto the roads and reduced MVCs; however, what portion of the fencing remains as a barrier given the lack of maintenance is unknown. Fencing also has the obvious negative side effect of further reducing landscape connectivity for many wildlife species in an already highly fragmented landscape and can trap wildlife on or within the fenced area if they manage to cross the fence.

Wildlife crossing structures have been shown to be effective in reducing vehicle collisions with wildlife and increasing landscape connectivity (Huijser et al. 2009). However, construction costs for these and other active forms of mitigation can be prohibitively expensive. In as developed a landscape as Massachusetts, construction of a sufficient number of wildlife over and under-passes to increase permeability of the road network is not practical.

Driver speed has been shown to greatly increase the probability and severity of vehicle collisions with moose and other wildlife. Traditional, permanent diamond warning signs with the image of a moose or other wildlife are believed to do little to affect driver behavior, reduce speed, and reduced vehicle collisions (Sullivan and Messmer 2003, Hedlund et al 2003). This is likely especially true if collisions with or sighting of the animals are rare, as with MVCs and moose in Massachusetts. Similarly, seasonal wildlife warning signs had limited effectiveness in reducing vehicle collisions with wildlife compared to more active mitigation methods (Huijser et al. 2009). However, in Massachusetts warning signs may actually be effective with urban drivers traveling in more rural portions of the state as the signs will be novel and may cause the driver to

take note. However, in Massachusetts signs warning of moose road crossing or MVCs have been relatively rare.

2.6.7 Reporting

The number of reported MVCs likely underrepresents the true frequency of MVCs in Massachusetts. Underreporting has been estimated to be 40% (Lavsund and Sandegren 1991), 50% (Dussault et al 2006), or up to 2 to 6 times the number of reported accidents (Child et al. 1991). Belant (1995) recommended standardized reporting of MVCs for Minnesota to enable MVCs to be used as an index for monitoring trends in the population. Annual reported moose-vehicle collisions, along with deer-hunter moose-sighting surveys, has been one of the best indices to monitor the growth and trends in the moose population in Massachusetts. However, variability in the reporting of MVCs limits the usefulness of this index and makes it difficult to determine if the recent decline in reported MVCs represents an actual trend in the state population or if it can simply be attributed to changes in reporting or recording of MVCs. This is extremely important, especially given the widespread concern about declining moose numbers along the southern extent of moose range in North America (Murray et al. 2006, Lenarz et al. 2010, Broders et al. 2012, DeCesare et al. 2014).

Greater accuracy in the spatial recording of MVCs would allow for more fine-scaled analysis of MVC locations. The fit of our models would undoubtedly improve with increased spatial accuracy. The values for speed limit and ADT would not change with increased accuracy, but measurement of slope and our habitat integrity variables likely would. By measuring slope out to 1.5 km and habitat integrity variables out several kilometers from our MVC locations, we partially minimized the influence of location error in the models; however, location error likely decreased model fit. Furthermore, increased accuracy would allow us to incorporate additional

habitat variables that likely influence where moose are crossing roads, such as proximity to forest harvest or wetland habitats (Wattles and DeStefano 2013a).

2.7 Management Implications

Our results emphasize the negative impacts of human-development and increasingly human-dominated environments on the ability of wide-ranging species to successfully move about the landscape. The greater proportion of the state's estimated moose population that are involved in MVCs compared to less developed portions of moose range and within the state the greater risk of MVCs in areas of higher human development underscore the impacts of high levels of human development on wildlife. The Connecticut River Valley and Coastal Plain are essentially non-moose habitat due to extreme habitat fragmentation and the density of high-speed and high-volume roads, which serve as lethal barriers to moose movements. In the Worcester and Berkshire Plateaus, state highways and interstates fragment the landscape, but not to an extent that has prevented occupation by moose. Moose interactions with class 1 and 2 roads have decreased survival in these ecoregions, as the risk of MVCs on these roads is very high, especially where they cross more intact blocks of habitat. Moose-vehicle collisions constitute the greatest known cause of mortality of moose in Massachusetts (MACFRU, unpublished data) and is possibly one of the main factors preventing further growth of the moose population. Additionally, the high proportion of MVCs in the state that result in human fatalities highlights the risk to the human population.

Our results can be used to draw inference on the impacts that the highly developed landscape of Massachusetts has on other wildlife species. While high speed and traffic volume roads pose a great risk to moose that attempt to cross them, moose are a large and highly vagile species that can cross roads rapidly. Species with lower mobility likely have even greater

mortality rates when attempting to cross roads and as a result, these roads may serve as population sinks or barriers to movements for some populations or species.

The high costs of alternative mitigation measures means that increasing public awareness of the risk of moose-vehicle collisions, with the goal of reducing driver speed, is likely the best method currently available to reduce MVCs. A recent collaboration between the Massachusetts Division of Fisheries and Wildlife, the Massachusetts Department of Transportation, and the MACFRU has centered on these goals, particularly in MVC "hot spots", where the risk is exceptionally high (~10% of total known location collisions per hot spot). The focus has been on the use of permanent warning signs placed at access points to highways in the hotspots. Additionally, mobile electronic messaging boards may be deployed during peak risk seasons. Whether increased signage in these hot spots will affect driver behavior and actually reduce MVCs remains to be seen. However, the low cost of installing signs relative to the savings from preventing even a single MVC strongly supports these efforts. Perhaps cooperation with local and state police departments to increase enforcement of speed limits and reduce driver speed would be the most effective strategy.

Given the current mitigation options at the disposal of wildlife and transportation departments, the density of roads, the volume of traffic, and the speeds vehicles travel, moose-vehicle collisions will continue to pose a threat to both moose and humans in Massachusetts. These conditions may mean that frequent and potentially deadly collisions are an unavoidable reality where large wide-ranging wildlife species live in human-dominated landscapes.

Tables

Table 2.1 Summary of annual moose-vehicle collisions (MVCs) reported for states, provinces, and nations reported in the literature, including; the size of the moose population, annual MVCs, percent of the moose population involved in MVCs, and the human fatality rate (HFR) from those collisions.

Country/ Province/State	Estimated Moose population	Annual MVC	Percent of population	HFR	Date	Citation
Massachusetts, USA	1000	30-50	3-5	0.7	2003-2012	This paper
Maine, USA	30,000 - 60,000	650	1-2	0.4	1995 - 2007	Wattles and DeStefano 2011
New Hampshire, USA	4,000 - 6,000	250	4-6	0.3	1995 - 2007	Wattles and DeStefano 2011
Vermont, USA	4,000 - 5,000	150	3-4	0.6	1995 - 2007	Wattles and DeStefano 2011
Norway	100,000 - 150,000	711 - 1,464	1.2	NA	1987 - 1993	Groot Bruinderink and Hazebroek 1996
Newfoundland, CAN	NA	168 - 460	NA	0.1	1983 - 1990	Oosenbrug et al. 1991
Newfoundland, CAN	150,000	616 - 897	0.4-0.6	0.26	1988 - 1994	Joyce and Mahoney 2001
Sweden	NA	4,000	1.8	NA	NA	Groot Bruinderink and Hazebroek 1996
Finland	NA	150	1.2	NA	NA	Groot Bruinderink and

						Hazebroek 1996
Minnesota, USA	4,300-6,800	24 - 31	0.4-0.7	NA	1993 - 1994	Belant 1995
British Columbia, USA	180,000	111 - 234	0.1	NA	1983 - 1990	Child et al. 1991
British Columbia, USA	180,000	700 (estimate)	0.4	NA	1983 - 1990	Child et al. 1991
Maine, USA	NA	583	NA	NA	1992 - 2005	Danks and Porter 2010
Kenai Peninsula, Alaska, USA	NA	112, 216	NA	NA	1977 - 1982, 1984 - 1989	Del Frate and Spraker 1991
Quebec	NA	161 - 300	NA	NA	1990 - 2002	Sebbane and Courtois 2000 (Ref in Dussault et al. 2006b)
Sweden	200,000 - 250,000	4,000 - 6,000	1.6-3	0.25-0.4	1980 - 1990	Lavsund and Sandegren 1991
Sweden		5,000		0.2-0.3	1990-1999	Seiler 2005
Alaska (rural)	NA	NA	NA	0.5	NA	Garrett and Conway 1999

					(citing Thomas 1995)
Anchorage, AK	450 (900)	100	11	0	1991-1995	Garrett and Conway 1999

Table 2.2 The density of roads (km/km2) of class 1-5 in each ecoregion and the mean average daily traffic (ADT) for that class of road in that ecoregion for Massachusetts.

	class 1		class 2		class 3		class 4		class 5		Overall
	density	ADT	density	ADT	density	ADT	density	ADT	density	ADT	
Worcester Plateau	0.03	31000	0.22	4300	0.13	1300	1.22	100	0.33	100	1.95
Connecticut River Valley	0.07	43000	0.38	8700	0.41	6000	2.72	300	0.35	100	3.99
Coastal Plain	0.14	79000	0.37	9100	0.51	4600	3.39	300	0.17	200	4.72
Berkshire Hills	0.01	23000	0.15	2700	0.08	800	0.63	100	0.43	100	1.32

Table 2.3 Description and source of data for variables used in modeling of moose vehicle collisions in Massachusetts.

Variable	Description	Source
Road class (class)	1. Interstate and major highways, 2. state highways, 3. major local arteries, 4. light duty roads, 5. unpaved roads	CAPS Roadline layer (www.masscaps.org, McGarigal et al. 2012)
Speed limit (speed)	Posted speed limit reported on EOTroadlines_arc layer. If speed limit was not posted we assigned speeds of 65, 50, 40, 30, and 25 mph (miles per hour) (104.6, 80.5, 64.4, 48.3, and 40.2 kph (kilometers per hour)) for class 1, 2, 3, 4, and 5 roads, respectively.	MassDOT 1:5000 Roads layer (MassGIS 2013)
Traffic volume (ADT)	Average daily traffic from the CAPS roads layer (www.masscaps.org).	CAPS Roadline layer (www.masscaps.org, McGarigal et al. 2012)
Slope (slope)	The mean slope of 8 - 1.5 km transects radiating at 0, 45, 90, 135, 180, 225, 270, and 315 degrees from MVC locations. Each of the 8 means was the mean of slope measurements every 30 m along the individual transects.	30 m Digital Elevation model (Mass GIS 2013)

Relief (relief)	The mean maximum relief recorded along the 8 transects used for the slope calculation.	30 m Digital Elevation model (Mass GIS 2013)
Connectivity (conn)	The mean connectivity within a circular buffer around each MVC location, measured from a 30 m resolution connectivity layer. We used a connectivity layer available at www.masscaps.org. (McGarigal et al. 2012)	CAPS Connectivity layer (www.masscaps.org, McGarigal et al. 2012)
Road density (road)	The density (km/km^2) of all roads within a circular buffer around each MVC location.	MassDOT 1:5000 Roads layer (MassGIS 2013)
Natural (nat)	The amount of forest and wetland habitat within a circular buffer around each MVC location.	2009 Landuse layer (MassGIS 2013)

Table 2.4 The distribution of known and unknown location moose-vehicle collisions (MVCs) by ecoregion and the distribution of MVCs by road class in each ecoregion of Massachusetts, 1980-2012.

| | Known location MVC | | | | | | | Unknown location MVC | |
| | Class | | | | | | Proportion | | Proportion |
	1	2	3	4	5	Total	by Ecoregion	Total	by Ecoregion
Worcester Plateau	54	115	6	9	2	186	0.56	46	0.51
Connecticut River Valley	17	13	4	3	0	37	0.11	15	0.16
Coastal Plain	22	13	5	5	0	45	0.14	11	0.12
Berkshire Hills	13	40	4	6	1	64	0.19	19	0.21
Statewide	106	181	19	23	3	332		91	

Table 2.5 Occurrence ratios of moose-vehicle collisions on roads of the 5 classes in each ecoregion. Occurrence ratios were calculated by taking the proportion of moos-vehicle collisions that occur on each road class and dividing by the proportion of that class of road in each ecoregion.

	Road Class				
	1	2	3	4	5
Worcester Plateau	19.53	5.41	0.50	0.08	0.06
Connecticut River Valley	25.03	3.74	1.06	0.12	0.00
Coastal Plain	16.06	3.68	1.03	0.15	0.00
Berkshire Hills	23.21	5.46	1.02	0.20	0.05

Table 2.6 Comparison of models used to predict the relative probability of moose-vehicle collisions in Massachusetts, one model for each ecoregion with the best model shown in bold. Included are number of variables (k), difference in Akaike information criteria for small sample sizes (AICcΔ), AIC weight (w), and log-likelihood values (LL).

	k	AICcΔ	w	LL
Worcester Plateau				
class + slope + nat5 + class*nat5	**7**	**0**	**0.75**	**-183.508**
class + slope + nat5	5	2.2	0.25	-186.753
Connecticut River Valley				
speed + ADT + slope + conn7.5 + ADT*conn7.5	**6**	**0**	**0.6975**	**-77.012**
speed + ADT + slope + conn7.5 + ADT*conn7.5 + ADT*speed	7	2.1	0.2502	-76.506
speed + ADT + slope + conn7.5 + ADT*conn7.5 + ADT*speed + speed*conn7.5	8	5.2	0.0523	-76.431
Berkshire Plateau				
speed + ADT + slope + nat10 + ADT*nat10 + ADT*speed	**7**	**0**	**0.779**	**-105.868**
speed + ADT + slope + nat10 + ADT*nat10 + ADT*speed + speed*nat10	8	2.5	0.221	-105.821

Coastal Plain*,**

class	**3**	**0**	**0.4038**	**-106.42**
class + conn10	**4**	**0.1**	**0.3893**	**-105.25**
class + conn10 + slope	**5**	**1.5**	**0.1873**	**-104.72**
class + conn10 + slope + class*conn10	7	6.1	0.0195	-104.23

* VIF >3 prevented consideration of models with speed and ADT

** final model weights for model averaging calculated without saturated model (0.412, 0.397, 0.191)

Table 2.7 Parameter estimates (± standard erro (SE)) and odds ratios for RSF models predicting moose-vehicle collisions in 4 ecoregions of Massachusetts, significant coefficients (*P*-value < 0.05) in bold (*P*-value <0.1 in italics). Class 3 was the reference category for class in models for the Worcester Plateau and Coastal Plain.

	Worcester Plateau (n = 186)					Berkshire Hills (n = 64)			
	Estimate (± SE)	Odds Ratio	Adjusted odds			Estimate (± SE)	Odds Ratio	Adjusted odds	
Intercept	6.67 (± 2.84)				Intercept	-4.86 (± 3.51)			
class1	7.00 (± 6.22)	1096.6	--		**speed**	**6.43e-02 (± 1.32e-02)**	1.1	--	
class2	-4.04 (± 3.59)	0.02	--		ADT	6.04e-04 (± 4.97e-04)	1.0	--	
slope	**-0.18 (± 0.06)**	**0.84**	--		**slope**	**-8.04e-02 (± 3.78e-02)**	0.92	--	
nat5	*5.90 (± 3.35)*	*365.0*	1.80	a	nat10	-6.05e-01 (± 3.83)	0.55	0.99	a
class1*nat5	-2.52 (± 1.57)	0.08	0.78	a	**ADT*nat10**	**1.39e-03 (± 6.81e-04)**	1.00	1.15	f
class2*nat5	**9.40 (± 4.21)**	**12088.4**	**2.56**	a	**speed*ADT**	**-1.74e-05 (± 3.54e-06)**	1.00	0.84	g
	CT River Valley (n = 37)					Coastal Plain (n = 45)			
Intercept	-6.86 (± 1.03)				Intercept	-4.15 (± 1.56)			
speed	**4.4e-02 (± 1.54e-02)**	**1.04**	**1.55**	b	**class1**	**4.32 (± 1.62)**	**74.8**	--	
ADT	*-5.2e-05 (± 2.8e-05)*	*1.00*	*0.95*	c	**class2**	**2.52 (± 1.35)**	**12.4**	--	

slope	**-1.65e-01 (± 6.53e-02)**	**0.84**	--		conn10	5.27 (± 12.24)	194.2	1.69	d
conn7.5	-5.96 (± 4.38)	0.003	0.55	d	slope	-0.021 (± 0.11)	0.98	--
ADT*conn7.5	**1.6e-03 (± 3.2e-04)**	**1.00**	**1.17**	e

a) natural in scale from 0 to 1, odds ratio for nat5 represents a 1 or 100% increase in proportion nat5, adjusted odds for 0.1 change in nat5

b) odds ratio for speed for 1 kph increase in speed, adjusted odds for 10 kph increase in speed

c) odds ratio for ADT for 1 vehicle per day increase in ADT, adjusted odds for 1000 vehcile per day increase in

d) odds ratio for conn7.5 for 1 unit increase in conn7.5, conn7.5 at a scale of 0 to 0.6, adjusted odds for 0.1 increase in conn7.5

e) odds adjusted up from 1 to 1000 vehichles per day for ADT and down from 1 to 0.1 for conn7.5

f) odds adjusted up from 1 to 1000 vehciles per day for ADT and down from 1 to 0.1 for nat5

g) odds adjusted up from 1 to 1000 vehicles per day for ADT and from 1 to 10 kph for speed

Figure 2.1 Annual moose-vehicle collisions from 1980-2012 reported to the Massachusetts Division of Fisheries & Wildlife.
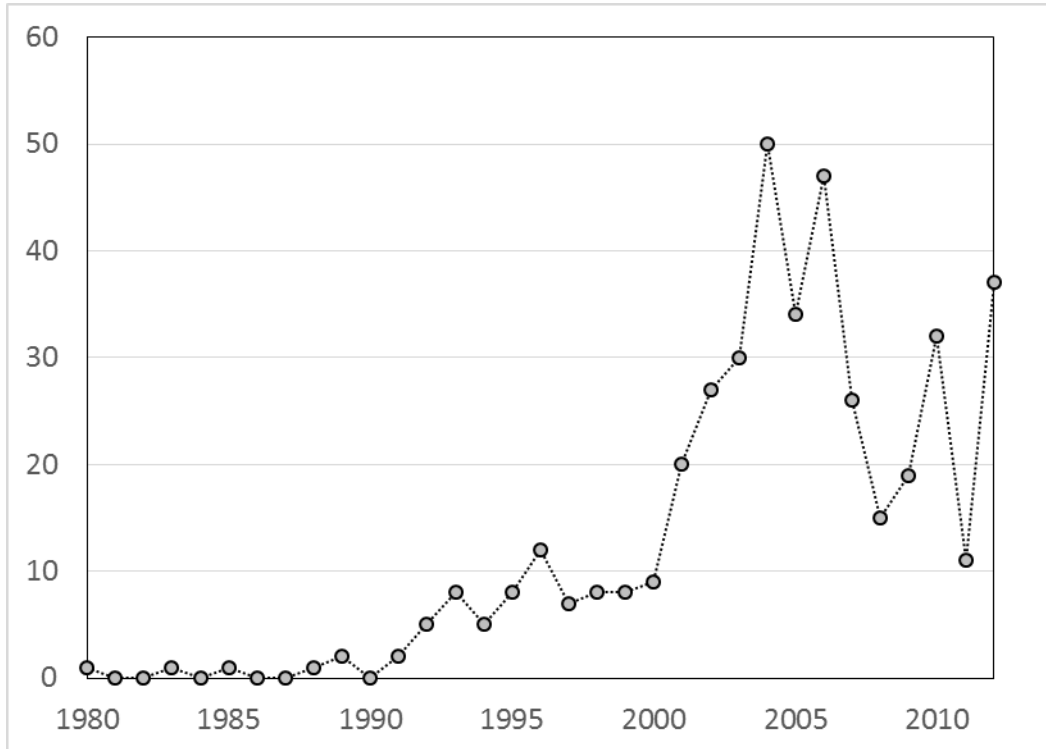
Figure 2.2 Digital elevation model of Massachusetts, USA. Study area and ecoregions are outlined in red. Reported moose-vehicle collisions are shown with blue dots. Class 1 and 2 roads are depicted with in black lines, class 1 roads are bolded.
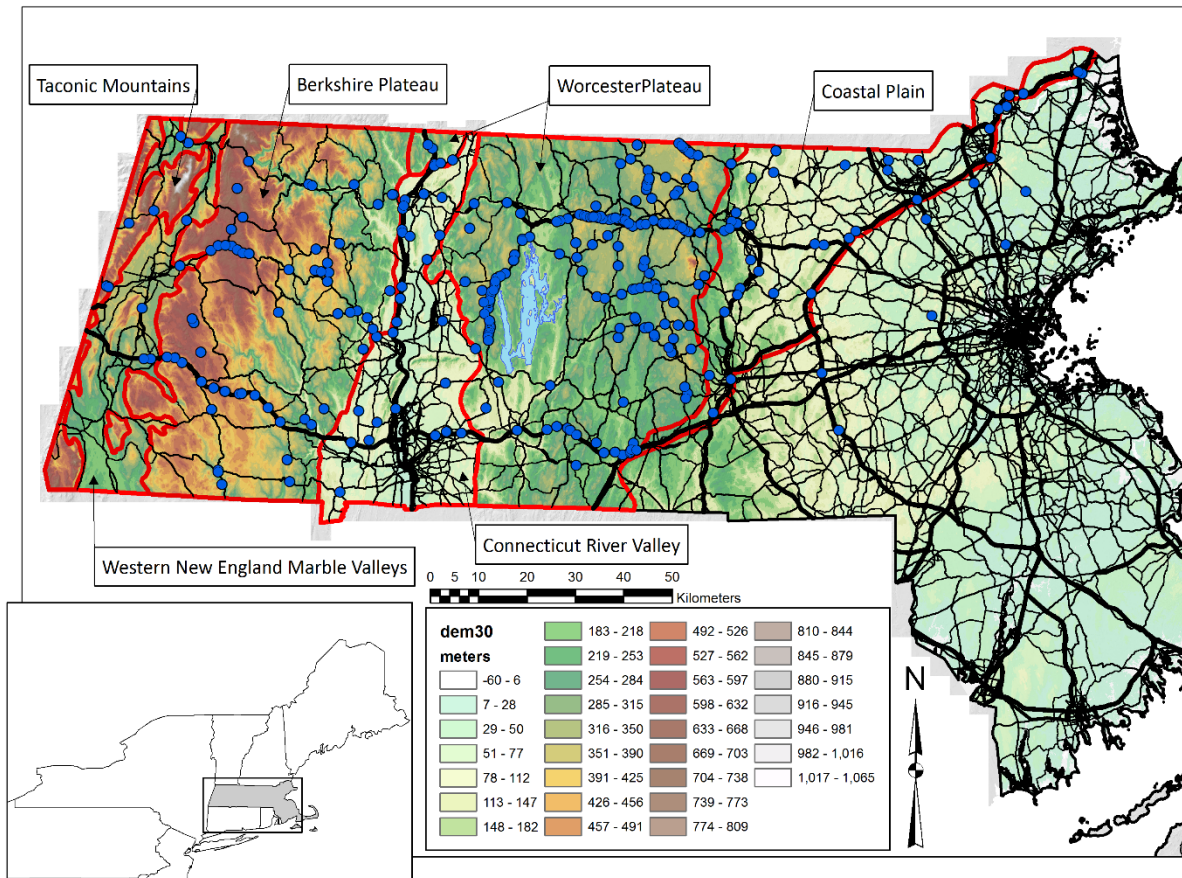
Figure 2.3 Human population density (individuals/km2) of Massachusetts towns (2010). Reported moose-vehicle collision locations shown as blue dots.
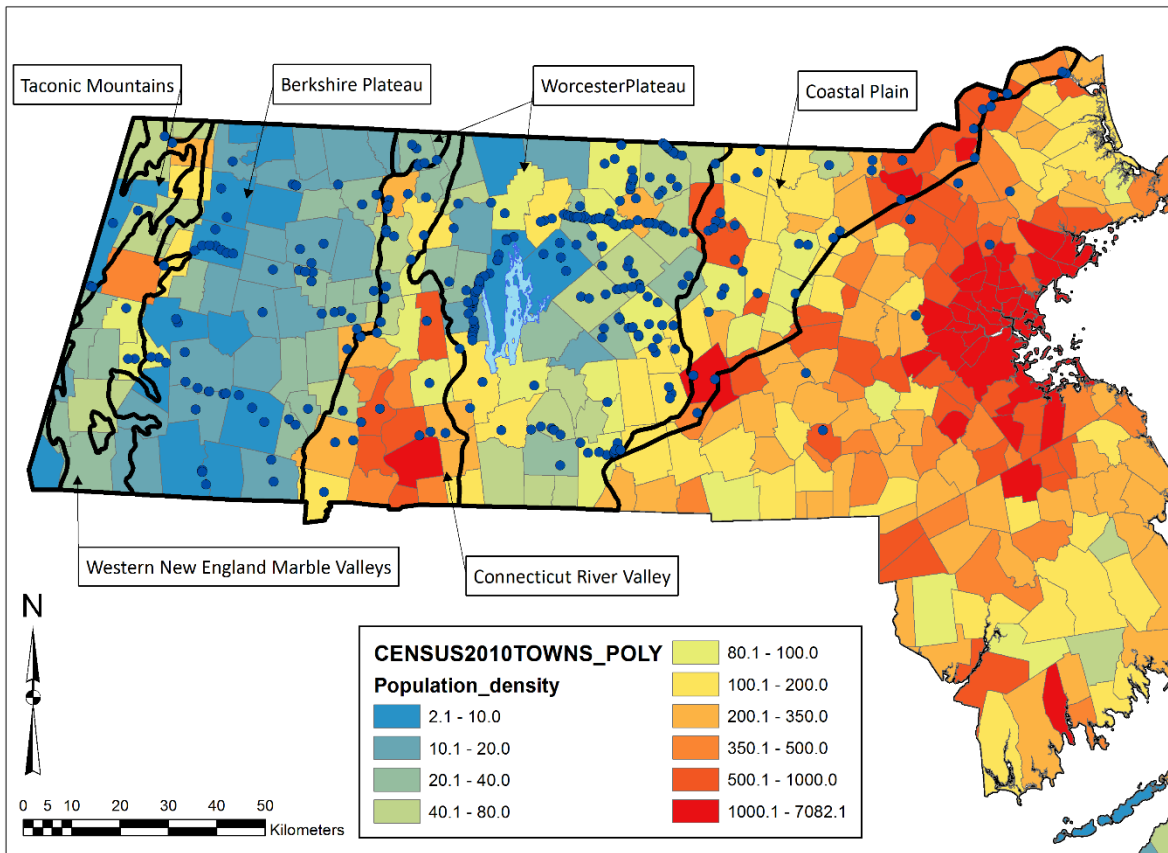
Figure 2.4 Average daily traffic (vehicles per day) of roads in Massachusetts. Reported moose-vehicle collision locations shown as blue dots.
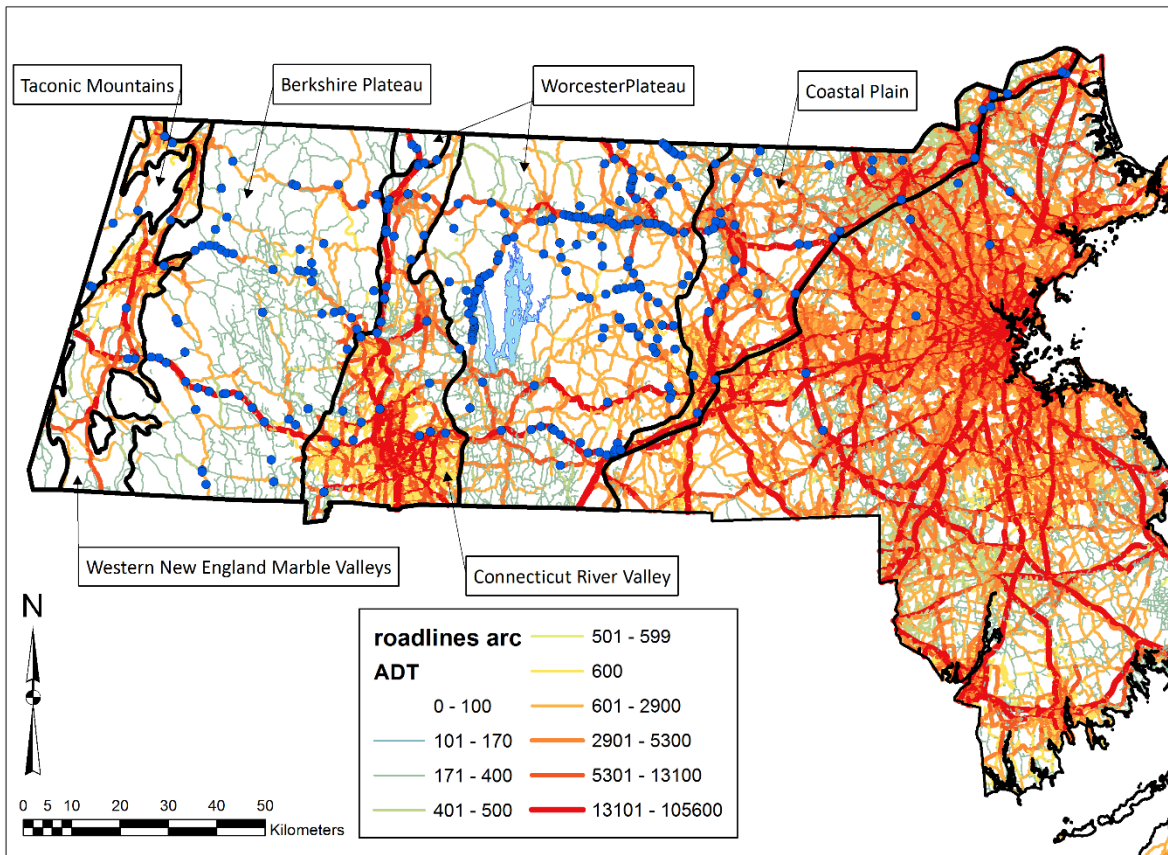
Figure 2.5 Total moose-vehicle collisions per month reported to the Massachusetts Division of Fisheries & Wildlife from 1980-2012.
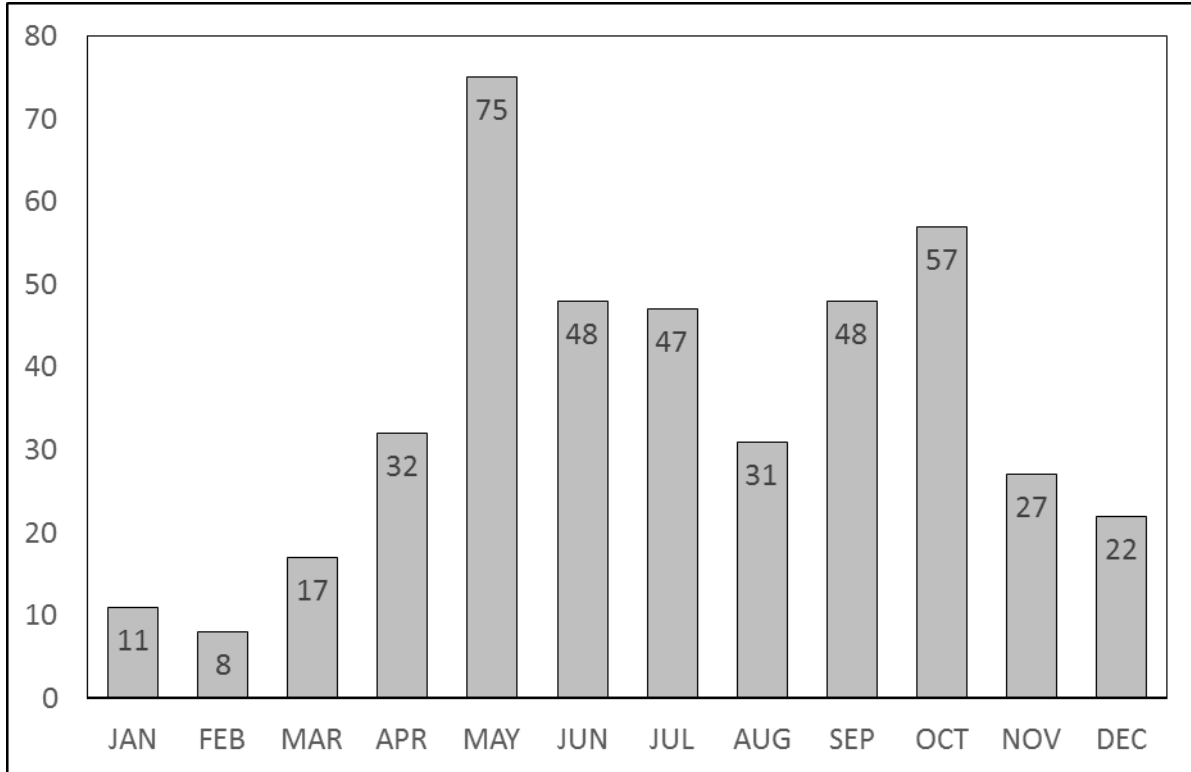
Figure 2.6 Location of Large Animal Response Team events from 1980 to 2008, moose relocations are shown with green dots and euthanizations with blue dots.
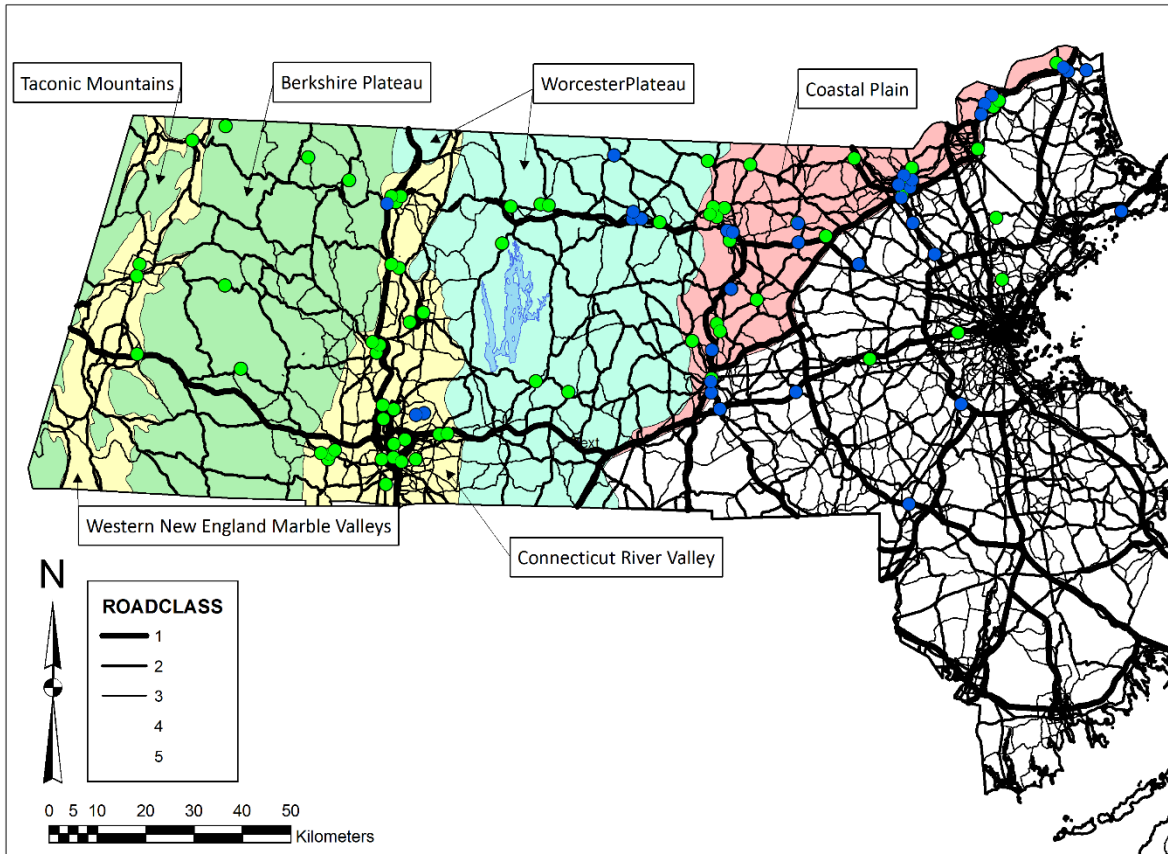
Figure 2.7 The interaction between the proportion of natural habitat around the roadway and road class on the relative probability of moose-vehicle collisions in the Worcester Plateau.
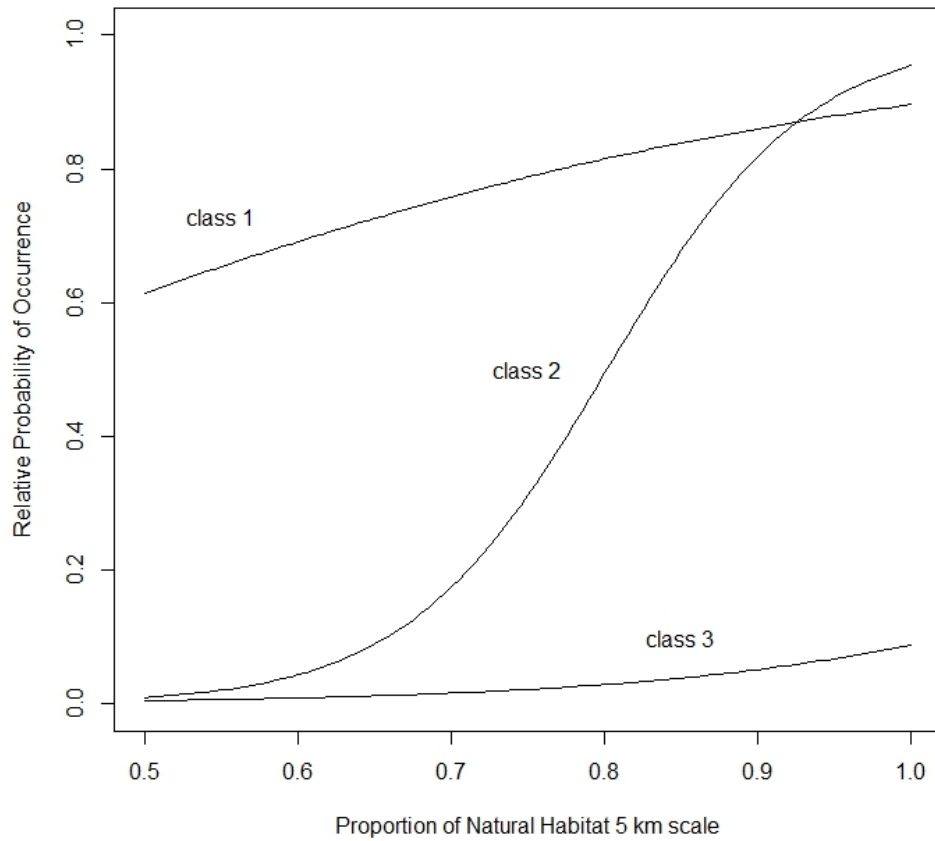
Figure 2.8 The interaction between traffic volume and connectivity on the relative probability of moose-vehicle collisions in the Connecticut River Valley (CTRV).
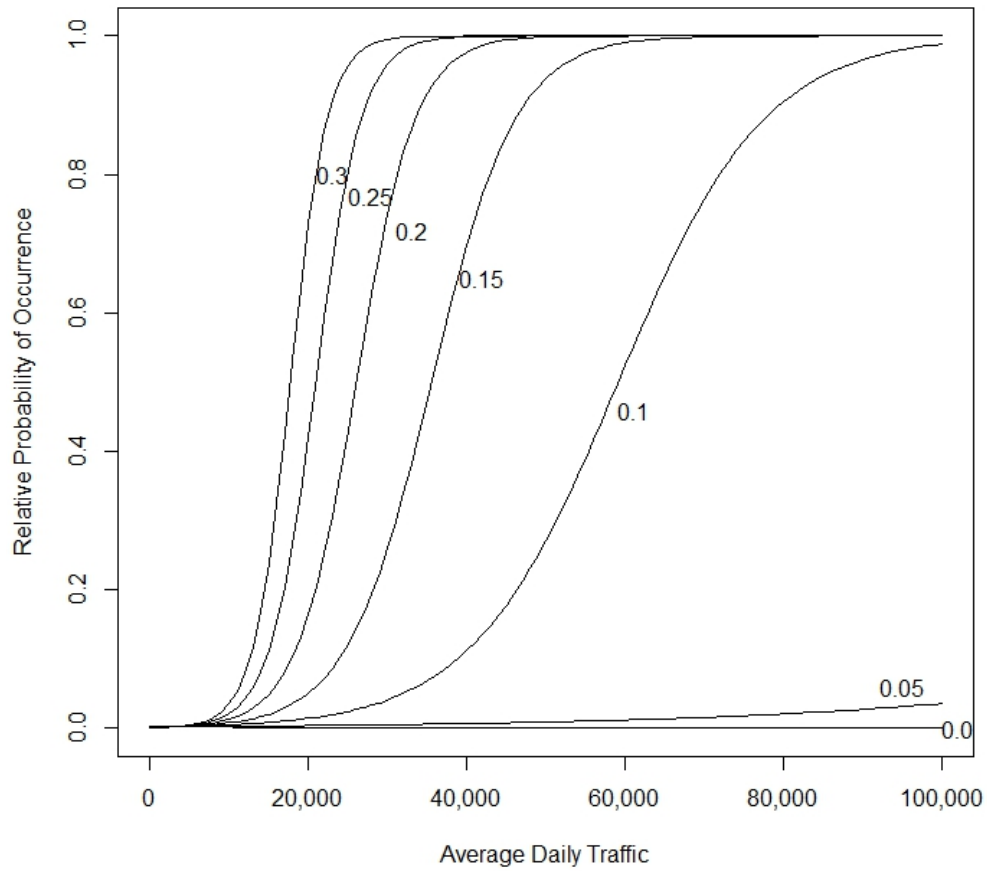
Figure 2.9 The interaction between speed limit and connectivity with traffic volume on the relative probability of moose-vehicle collisions in the Berkshire.
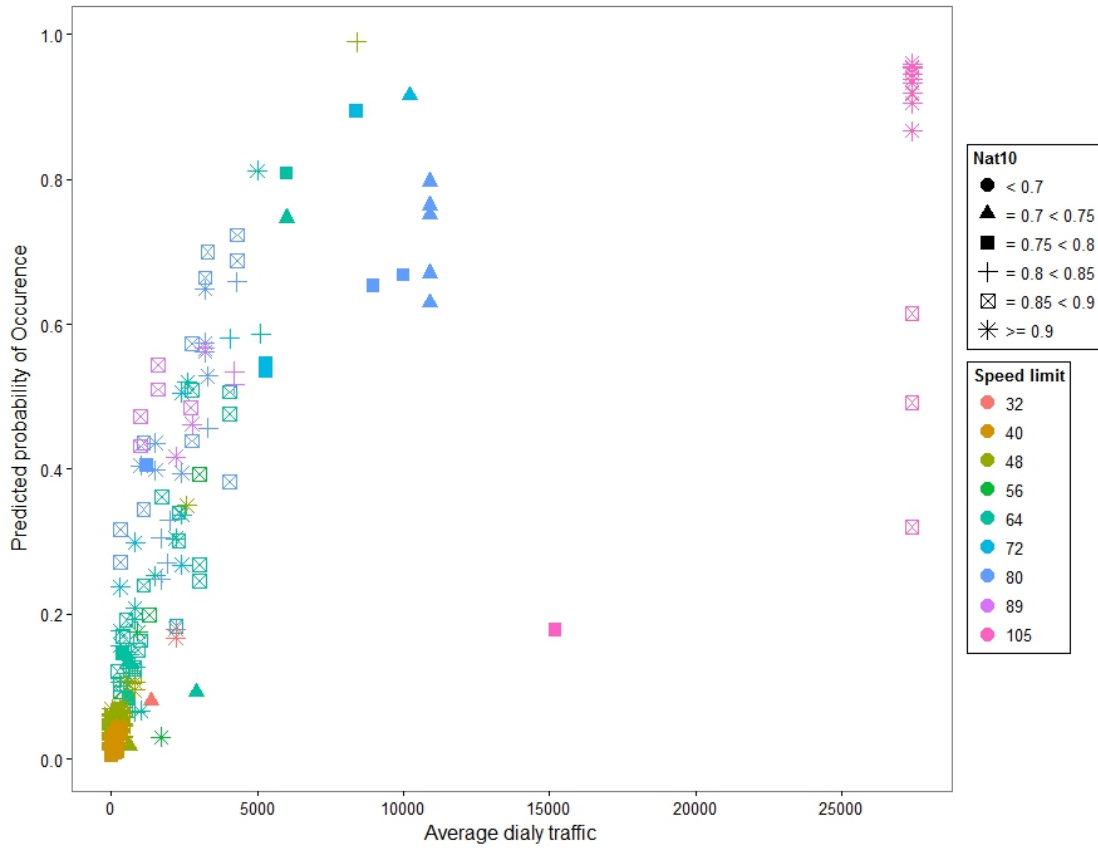
Figure 2.10 The relative probability moose-vehicle collisions on class 1, 2, and 3 roads in relationship to connectivity in the Coastal Plain.
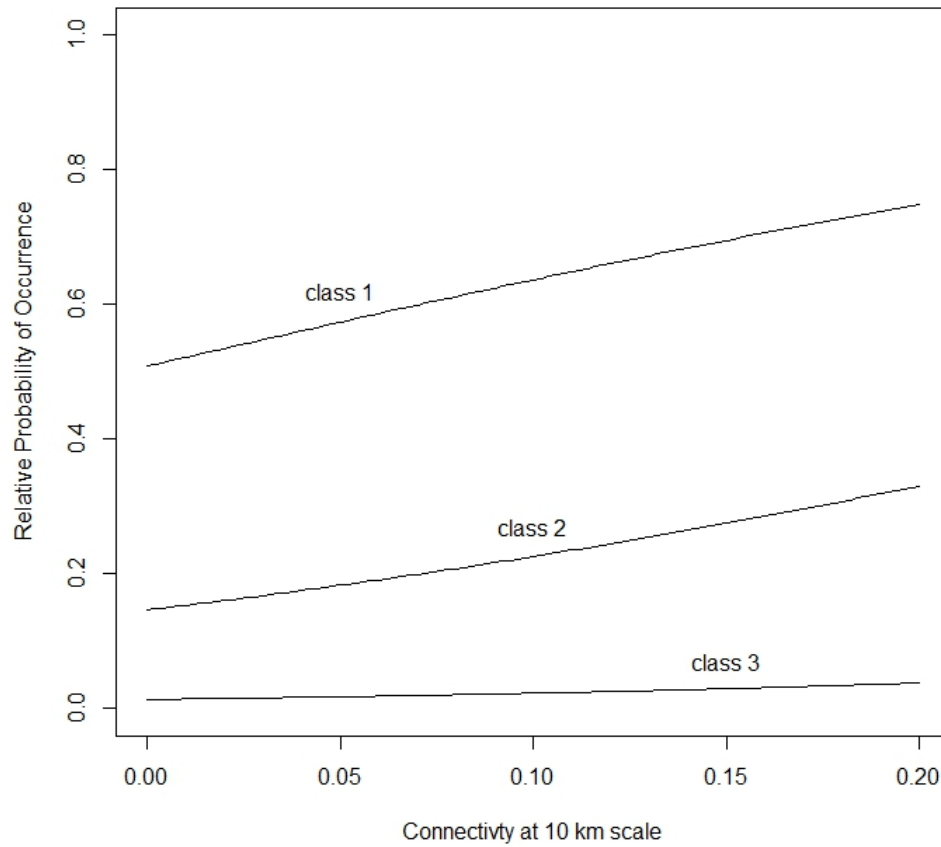
CHAPTER 3

THE INFLUENCE OF A HIGH-DENSITY ROAD NETWORK ON HABITAT SELECTION AND MOVEMENTS OF MOOSE

3.1 Abstract

Road networks and the disturbance associated with vehicle traffic can have major impacts on wildlife and alter animal behavior, movements, and habitat selection. Roads fragment the landscape, which can reduce wildlife movements and therefore landscape connectivity. Additionally, road avoidance by wildlife can reduce the amount of suitable habitat that is available to animals. Massachusetts is one of the most densely populated states in the United States and has an extremely dense and heavily used road network. I used correlated random walks and resource selection functions to analyze movement and location data from collared moose in Massachusetts to determine how the road network influenced moose movements and habitat selection. The road network had a strong negative effect on both the movements and habitat selection patterns of moose. Moose crossed roads at a much lower rate than predicted by the simulated movement paths and greatly reduced their habitat use near roads. Road avoidance increased with increasing disturbance intensity associated with roads, such as higher traffic volumes and times of day when traffic and human activity is greatest. Overall, roads were a major factor determining what portions of the landscape in Massachusetts moose considered suitable habitat and how they moved between habitat patches.

3.2 Introduction

The expansion of roads and road networks are one of the most common mechanisms of habitat fragmentation throughout the world. Even in relatively contiguous habitats, habitat

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fragmentation can occur where roads and corridors bisect the landscape. The fragmentation by roads can affect almost all sizes and classes of animals, and can result from a single road passing through an otherwise intact ecosystem or by a high-density road network that fragments a landscape into many smaller patches (Fahrig and Rytwinski 2009).

Roads can have many direct and indirect effects on wildlife populations, including reducing the survival of individuals and altering population dynamics, influencing movements and habitat selection patterns, and decreasing gene flow and genetic diversity (Foreman and Alexander 1998, Coffin 2007, Balkenhol and Waits 2009). Roads and associated vehicle collisions can be a direct cause of mortality for wildlife and in many instances is one of the greatest known causes of mortality for some species. For example, it is estimated that over a million cervid-vehicle collisions occur each year in Europe and North America (Groot Bruinderink and Hazebroek 1996, Grosman et al. 2011 and references there in). Roads can serve as barriers that prevent or restrict movement between blocks of habitat, which can reduce or prevent the use of otherwise suitable habitat and functionally isolate habitat patches (Riley et al. 2006). If barriers to movement are great enough, they can prevent gene flow and completely isolate portions of populations (Riley et al. 2006). Fragmentation also directly reduces both the size of habitat patches and the amount of interior or core area habitat that is preferred by many species, through the road effect zone (Forman et al. 2002). The road effect zone can be associated with direct habitat alteration along patch edges, characterized by changes in microclimate and species composition of both plants and animal assemblages. Edge effects for wildlife species can also take the form of avoidance of vehicle traffic, human activity, noise, and other factors close to roadways. In many cases, roads that penetrate intact blocks of habitat also

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provide access to humans that result in other impacts, such as direct mortality from hunting or poaching, or habitat degradation through logging or development.

Moose (*Alces alces*) historically occupied the forests of Massachusetts and southern New England but were extirpated in this portion of their range by the mid to late 1800s, primarily through unregulated hunting and clearing of forests for agriculture (Wattles and DeStefano 2011). Moose populations in the northeastern United States have since rebounded and moose have reoccupied much of their historic range (Wattles and DeStefano 2011). However, in their absence, the landscape was drastically altered. While the region had largely undergone reforestation after farms were abandoned, it also became one of the most human-dominated areas in the United States (Hall et al 2002).

Massachusetts is one of the most densely populated states in the country (DeStefano et al. 2005, U.S. Census Bureau 2010) and has an extremely extensive and dense road network that fragments the largely forested landscape (Fig. 3.1). Expansion of suburban areas outward from cities continues at a rapid rate (5.25 hectares of land developed per day from 2005 to 2013; Lautzenheiser et al. 2014). People commute long distances to and from work, which adds greatly to the growing number of vehicles on the roadways, which now bisect the forested habitat of previously rural portions of Massachusetts.

Moose are a large, highly mobile, and wide-ranging species with large home ranges (Wattles and DeStefano 2013b), which in a landscape like that of Massachusetts, inevitably encompass roads and human development. As moose move about and attempt meet their life history needs, they must choose whether or not to select cover types near roads and whether or not to cross roads. While roadways were suspected to have a major impact on wildlife, including moose (Forman and Deblinger 2000), no studies had been conducted to examine the direct effect

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of the road network on the movement and habitat selection of wildlife. Understanding how road networks affect wildlife is essential for conserving wildlife populations and wildlife diversity as human development continues.

Wattles and DeStefano (2013b) showed that moose avoided more highly developed areas at the landscape scale (home range selection; 2nd order habitat selection according to Johnson 1980) and at coarse scales within home ranges (3rd order selection). Additionally, Wattles (2014) reported a disproportionately high risk of moose-vehicle collisions on high speed and high traffic volume highways compared to all other classes of roads in Massachusetts.

We used Global Positioning System (GPS) technology to further investigate the relationships between road characteristics and moose movements and habitat use in Massachusetts. Our objectives were to determine how the high density, high traffic volume road network influenced the movements and fine-scaled habitat selection patterns of moose. We hypothesized that roads would influence both the movements and habitat selection patterns; specifically, that moose would avoid crossing roads and avoid using areas adjacent to roads. We hypothesized that the magnitude of the road effect would vary by road type, season, and time of day, and that avoidance would increase with increasing traffic volume, speed, and in areas of higher road density.

3.3 Study Area

Our study area was located in western two thirds of Massachusetts, USA and adjacent portions of southern Vermont and New Hampshire (between 42° 9' and 42° 53' N latitude and 71° 53' and 73° 22' W longitude). Topography is dominated by glaciated hills with abundant small stream valleys, lakes, ponds, and palustrine wetlands whose size and nature varies with

changes in beaver (*Castor canadensis*) activity. The central and western sections of the study area are separated by the Connecticut River Valley, which runs N-S through west-central Massachusetts. Elevation ranges from 100 m above sea level in the Connecticut River Valley, to 425 m in the hills of central Massachusetts, to 850 m in the Berkshire Hills of western Massachusetts.

The western two-thirds of Massachusetts was >80% mixed deciduous, second- or multiple-growth forest, much of it resulting from regeneration of farm fields abandoned in the mid-to-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 hardwoods, northern hardwoods-eastern hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*), transition hardwoods-white pine-hemlock, and central hardwoods-hemlock-white pine (see DeGraaf and Yamasaki [2001] and Wattles and DeStefano [2013a] for a more detailed description of forest types). Transitions between forest types can be gradual or distinct depending on localized physiography, climate, bedrock, topography, land-use history, and soil conditions, resulting in a patchwork of forest types and species groups (Westveldt et al. 1956, DeGraaf and Yamasaki 2001). Early successional habitat was created primarily through timber harvesting, and occasionally through wind and other weather events. During 1984-2000, about 1.5% of the forest was harvested annually, consisting of small (mean = 16.5 ha) cuts of moderate intensity (removal of 27% of timber volume) widely distributed on the landscape (Kittredge et al. 2003, McDonald et al. 2006). The pattern of forest harvest and transitional forest types, as well as a history of glaciation, provided a patchy mosaic of well-interspersed forest types, age classes, and wetlands.

Massachusetts has one of the highest densities of humans, human development, and road densities in the United States (5th most densely populated state with 324 people/km^2 statewide)

(DeStefano et al. 2005, U. S. Census Bureau 2010, Fig 1). Mean road densities in the two portions of the state where the majority of moose occur are 1.95 and 1.32 km/km^2, respectively, for the Worcester Plateau and Berkshire Hills. Road densities in the more highly developed Connecticut River Valley and eastern Massachusetts are 3.99 and over 5 km/km^2, respectively.

3.4 Methods

3.4.1 Moose Capture and Telemetry

We captured adult (>1 yr old) moose by opportunistically stalking and darting them from the ground between March 2006 and November 2009. Moose were immobilized using either 5 ml of 300 mg/ml or 3 ml of 450 mg/ml xylazine hydrochloride (Congaree Veterinary Pharmacy, Cayce, South Carolina, USA) administered from a 3 or 5 cc Type C Pneudart dart (Pneudart, Inc., Williamport, Pennsylvania, USA). We used Tolazolene (100 mg/ml) at a dosage of 1.0 mg/kg as an antagonist. Moose were fitted with GPS collars, either ATS G2000 series (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) or Telonics TWG-3790 GPS collars (Telonics, Inc., Mesa, Arizona, USA). We programmed the collars to attempt a GPS fix as frequently as possible while allowing the battery life to extend for at least 1 year; depending on the collar, a GPS fix was attempted every 135, 75, or 45 minutes. Collars were equipped with very high frequency (VHF) transmitters, mortality sensors, and automatic mechanisms that released the collars either at a low battery state or at a preprogrammed date. Capture and handling procedures were approved by the University of Massachusetts Institutional Animal Care and Use Committee, protocol numbers 25-02-15, 28-02-16, and 211-02-01.

3.4.2 Road Crossings and Correlated Random Walks

We analyzed the road-crossing frequency of moose by quantifying the intersection rate of their movement paths with Geographic Information System (GIS) road layers for Massachusetts (Conservation Assessment and Prioritization System (CAPS)) and adjacent portions of Vermont (Vermont Center for Geographic Information) and New Hampshire (New Hampshire Geographically Referenced Analysis and Information Transfer System; NH GRANIT). All GIS work was performed using ArcGIS 10.1 (ESRI 2011).

We classified roads into 6 categories: class 1 (Expressways, which were roads with multiple lanes in each direction), class 2 (Primary state highways), class 3 (secondary highways or major local arteries), class 4 (Light duty roads previously classified as class 4 with >200 vehicles per day average daily traffic (ADT), class 5 (Light duty roads previously classified as class 4 with ≤200 ADT), and class 6 (forest roads and roads with ADT <10).

We used correlated random walks (CRW) (Turchin 1998) generated with the "movement.simplecrw" tool in Geospatial Modelling Environment (Beyer 2012) to represent the expected distribution of moose road-crossing rates under the null model of no road effect (Beyer et al. 2013). For all analyses we split the data into 3 seasons based on differences in seasonal movement rates (Wattles and DeStefano 2013b): summer (16 April – 31 August), fall (1 September – 31 October), and winter (1 November – 15 April). We initiated the correlated random walks (n = 100 for each moose-season) at the first actual moose location for that season. Subsequent locations were determined by randomly drawing a step length and turn angle from the seasonal distribution of step lengths and turn angles of that moose for that season, until the number of steps equaled the number taken by the moose. We restricted the CRWs to the seasonal minimum convex polygon (MCP) home range of the moose plus a 1,000 m buffer. We use the

buffered MCP home range rather that the MCP (Beyer et al. 2013) because roads outside the MCP could serve as boundaries to movement that the moose were reluctant to cross. Using only the MCP would exclude those roads from the analysis and prevent us from determining their effect on moose movement. One thousand meters represents a distance that moose could easily travel within one GPS fix sampling interval.

We used mixed-effect linear regression with the package lmerTest (Kuznetsova et al. 2014) to compare the road-crossing rate of our collared moose with the mean of the 100 CRW paths for each moose-season. We used Program R version 3.0.1 for all statistical analyses (R Development Core Team 2005). For all models, we included the moose ID, a variable to identify each individual moose, as a random intercept to pair the crossing rate of each moose with the associated crossing rate for its seasonal CRWs, and to account for repeated measures on an individual (Gillies et al. 2006). For each season and road class, we compared saturated and reduced models for the road-crossing rate using Aikaike Information Criteria (AIC) difference for small sample sizes (AICc) and Akaike weights (*w*) (Burnham and Anderson 2004). The saturated model included the density of that road type in the animal's buffered home range, a variable named "moose" stating whether the crossing rate was associated with the real moose or the CRW, and the interaction between density and moose. We assessed model fit using pseudo-R squared after Nakagawa and Schielzeth (2013) and the package MuMin (Barton 2014). Additionally, we compared step lengths when moose crossed roads to the mean and 95th quantile of all movements step, including road crossings, to determine if moose altered their movement rates when traversing roads.

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3.4.3 Habitat Selection Relative to Road Network

We modeled within home range habitat selection (3rd-order, Johnson 1980) with and without a roads variable to determine if the road network influenced habitat selection by moose. We calculated mixed effect (Zuur 2010) resource selection functions (RSF) using a use:availability framework (Manly et al. 2002) and assumed the exponential form of the model (Johnson et al. 2006). We used mixed effect logistic regression to estimate model coefficients (β_i) for the fixed effects (x_i) representing the relative probability of use (w) with the equation:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + ... + \beta_k x_k + y_i).$$

Where y_i is the random effect of moose i.

We based availability for each animal on a random sample of locations generated within the animal's annual MCP home range, plus a 1,000 m buffer to account for habitat available along the periphery of the home range. We buffered all locations, then merged the buffer with the MCP to define availability, which represented habitat that was easily accessible to the individual. This sampling resulted in 1,175-1,527 random locations per individual.

To determine the influence of the roads on moose habitat selection, we created kernel density surfaces (30 m resolution) of the roads network in our study area. We allowed the magnitude of the road affect to vary by road class by assigning weights to each of the 5 road classes (weight = 1 for class 6 roads, 10 for class 5, 25 for class 4, 50 for class 3, and 100 for class 2 or weight = 0 for all road types for a model with no difference among types). The weight assigned to each road type represented the number of times each road of that type was counted when generating the kernel surfaces. For each combination of weights, we created kernels surfaces at 5 scales using smoothing parameters of 250, 500, 750, 1,000, and 1,500 m. We

extracted the values from the resultant kernel surfaces to our moose and random datasets to represent the road effect at each location.

We generated kernel surfaces with several combinations of weights and scales and calculated road-only RSFs where selection was predicted by a single variable "roads". We used a random intercept and random slope model, which takes into account repeated measures on an individual and allows for variation in the response to roads by individual moose (Gillies et al. 2006). For each season and period of the day, we used AIC difference and weight (w) to identify the best weight-scale combination (Burnham and Anderson 2004). Based upon the combinations of weights supported in the first set of candidate models we iteratively changed the weights assigned to the various roads classes and repeated the process to achieve the best combination of road weights and scale to represent roads in the model. We removed 2 animals from the analysis due to their disproportionate effect on model coefficients. These 2 animals nearly exclusively used large blocks of protected habitat in state forests and water-supply areas. As a result, their avoidance of roads was extremely high and inclusion of them in the models resulted in population level coefficients for roads that far exceeded the individual coefficients (random slopes) for all of the remaining animals in the analysis.

After finding the best road-only model we ran a habitat-only model that contained 7 categorical cover types (regeneration [logged areas <25 years old], mature deciduous forest, mature mixed coniferous-deciduous forest, mature coniferous forest, wooded wetlands, open wetlands, and other [open and developed areas]). We manually assigned cover types to used and random locations through examination of orthophotography and other GIS layers (Wattles 2014 chapter 1). The habitat-only model included a random intercept to account for repeated measures on an individual (Gillies et al. 2006). Finally, we created 2 global models that contained both the

road and habitat variables, one included an interaction between roads and habitat the other did not. The global models included a random intercept and random slope for roads. We used AIC to determine the best overall model between the 2 global models, the roads-only, and the habitat-only models.

Akaike information criteria can be used to select the best fitting and most parsimonious of the candidate models; however, it does not provide information on how well the models fit the data thus, we used k-fold cross-validation (Boyce et al. 2002) to evaluate model fit. This method uses subsets of the data, withholding 20% of the data to test models generated with the remaining 80%, and then generates Spearman's rank correlation coefficients (r_s), with high r_s indicative of good model fit.

3.5 Results

3.5.1 Capture and Deployment of GPS Collars

We deployed GPS collars on 26 adult moose (7 females and 19 males). Of the 26, we excluded 5 from the analysis due to mortality, suspected infection with brainworm (*Parelaphostrongylus tenuis*), or collar failure, resulting in 21 collared moose (5 females and 8 males in central and 8 males in western Massachusetts). We recaptured and recollared 9 moose when the batteries in their initial GPS collars ran low. We obtained 127,408 locations of the 21 moose used in this study, with an overall fix rate of 85%.

3.5.2 Road Crossing and Correlated Random Walks

We documented 9,162 road crossings in 87 total moose-seasons (number of moose x number of seasons; 428 for class 2, 121 for class 3, 1,482 for class 4, 818 for class 5, and 6,313 for class 6 roads. Observed road crossing rates varied by season and increased as seasonal

movement rates increased, from lowest in winter, to moderate in summer, to highest in fall ($\chi^2 >$ 10, df = 2, P – value < 0.01, for all road classes; Table 3.1, Fig. 3.2-3.4; Wattles and DeStefano 2013b). Therefore, to aid in interpretation of the seasonal response to roads we ran separate models for each season-road class combination.

Moose displayed a strong avoidance of roads of all types and crossed much less frequently than predicted by the null model (simulated CRWs) for most season-class combinations (Tables 3.1-3.2, Fig. 3.2-3.4). There were exceptions to this, however: moose showed no avoidance of class 4 roads in summer, minimal avoidance of class 6 roads in winter, and no response to class 6 roads in summer and fall (Table 3.2, Figs. 3.2-3.4). The null model predicted a linear increase in the crossing rate of roads of all classes with increasing road density within the buffered home range. In most season-class combinations, however, the actual crossing rate by moose was lower and increased at a lower rate with increasing road density than predicted by the null model (no road effect). As a result, model selection supported the saturated models for most seasons (Tables 3.2-3.3 (m1- rank 1), Figs. 3.2-3.4). In these season-road combinations at low road density, the crossing rate by moose was very low and similar to the null model, but as road density increased the difference in crossing rate between the simulated and real moose increased. The crossing rate for class 6 roads in winter and class 2 and 3 roads in fall were lower than predicted by the null model, but there was no difference in the rate of increase with increasing road density (Tables 3.2-3.3 (m2 rank 1), Figs. 3.2-3.4). The crossing rate of class 4 and 6 roads in summer and the crossing rate of class 6 roads in fall were not different than the null model ((Tables 3.2-3.3 (m3 rank 1), Figs. 3.2-3.4) indicating no avoidance of these road types during those seasons. Psedo- R^2 values for crossing rate models were very good, indicating strong explanatory power. Psedo- R^2 for fall class 6 roads model was 0.511,

while the Psedo- R^2 for all other seasonal models ranged between 0.678 and 0.898. Moose also altered their rates of movement when crossing roads: step lengths for road crossings were greater than the 95th quantile of movements during all seasons (Fig. 3.5).

3.5.3 Habitat Selection Relative to Road Network

In Massachusetts, roads had a significant influence on habitat selection by moose. Global RSF models that included the interaction between habitat and road variables were the highest-ranking models for all seasons and times of day (Tables 3.4-3.5). Models that did not include the road-habitat interaction, as well as the road-only and habitat-only models, received much less support. Additionally, multi-model inference indicated that there were seasonal and diel differences in the influence of the road and habitat components in predicting habitat selection patterns. The road network had a greater influence than cover type on diurnal habitat selection patterns in summer and fall and both diurnal and nocturnal habitat selection in winter. For these seasons-period combinations the roads only model performed much better than the habitat only model in predicting moose habitat selection (AIC $w < 0.001$ for habitat only models, when only the road-only and habitat-only models were considered). However, the influence of roads on nocturnal habitat selection in summer and fall was secondary to the influence of cover type (AIC $w < 0.001$ for road-only models, when only the road-only and habitat-only models were considered).

There was also a difference in the magnitude of the road effect on diurnal and nocturnal habitat selection patterns. Model selection supported models with smaller spatial scaling during the day in summer and fall (500 and 1,000 m, respectively) compared to at night (1,500 m). Kernels created at smaller scale resulted in very strong road avoidance at close proximity to the roadway and resulted in probability of selection maps with very low probability of use close to

roads (Figs. 3.6-3.7). Models of the road affect created with larger scale kernels resulted in a much lower difference in the relative probability of selection close to versus far from roads, which is what occurred at night in summer and fall (Fig. 3.8).

Multi-model inference also supported the hypothesis that roads with greater traffic volumes and speeds of travel would have a greater negative impact on habitat selection adjacent to the roadway. Models with variable weighting by road class performed far better than equal weight models and road weights increased as expected with increasing class (Table 3.6). The effect of increased weights was to reduce the relative probability of selection adjacent to higher weighted roads. Road weights were similar for all seasons and diel periods, with the most variation being in the effect of class 6, forest, and low traffic volume (ADT < 10) roads. There was no effect (weight = 0) for class 6 roads in fall and at night in summer. The effect of these roads was 5 during the day in summer and 20 both day and night in winter.

K-fold cross validation showed good model fit, mean r_s of 0.741, 0.969, 0.970, 0.991, 0.930, and 0.977 for summer day, summer night, fall day, fall night, winter day, and winter night, respectively.

3.6 Discussion

Roads had a clear two-fold influence on the movements and fine-scale habitat selection patterns of moose in the highly developed landscape of Massachusetts. Expected between-patch movements and, as a consequence, landscape connectivity were reduced, as was the overall area of suitable habitat. Moose tended to avoid roads and the areas adjacent to roads. Avoidance was positively related to disturbance intensity as indicated by the difference in strength of diurnal versus nocturnal road avoidance, and the increased weights for higher classed roads in RSF models. Additionally, the higher rates of movement moose exhibited when crossing roads

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indicated that moose attempted to move as quickly as possible through developed portions of the

landscape and reestablish a secure distance from roads after crossing. These results, combined

with the coarse scale avoidance of areas of higher road density reported by Wattles and

DeStefano (2013b), indicate that the road network is a strong determining factor of moose

occurrence and movements in the state.

There is general agreement that the avoidance that moose and other ungulates have of

roads, developments, and human activity is akin to antipredator behavior and varies with the

intensity of disturbance (Lima and Dill 1990, Frid and Dill 2002, Creel et al. 2005, Dodd et al.

2007, Lykkja et al. 2009, Elgard et al. 2012, Leblond et al. 2013, Nuemann et al. 2013).

However, attraction to roadways to exploit preferred habitat (e.g., timber harvest units or

wetlands along roads; Dodd et al. 2007, Rea et al. 2010), avoid predators (Berger 2007, Laurian

et al. 2012), or obtain rare resources (e.g., salt, young vegetation; Fraser and Thomas 1982,

Miller and Litvaitis 1992, Laurian et al. 2008, Grosman et al. 2011) has also been reported.

Laurian et al. (2012) reported greater avoidance of forest roads than of highways by moose in

Quebec, revealing the complexity in the relationships between the avoidance of risk or

disturbance and the influence of other factors in the behavior of wildlife. They attributed the

greater use of highway verges to an attraction to sodium deposits associated with roadway de-

icing, as well as avoidance of predators by females with calves (see also Berger 2007). The

avoidance of forest roads by moose was attributed to use by hunters and wolves. Despite the

common reporting of attraction of moose to roadside salt licks to obtain sodium (Fraser and

Thomas 1982, Miller and Litvaitis 1992, Laurian et al. 2008, Grosman et al. 2011), we did not

observe this behavior in any of our moose. Additionally, moose in Massachusetts are free from

the selective pressure of predation by wolves (*Canis lupus*) or from human hunters. Therefore, the response to roads we documented was directly attributable to disturbance intensity.

Depending on the diel period and the corresponding amount of vehicle traffic and human activity, roads and cover type (the two factors considered in our RSF models) influenced habitat selection in a hierarchical manner. This hierarchy provides insights into the manner in which roads influence moose behavior in a human dominated landscape. During the day, when the perceived safety risk associated with roads was greater, the road network was the main driver of moose habitat selection, determining what portions of the landscape moose considered suitable habitat. Within those suitable areas, selection was driven by cover types used to provide food, water, and shelter. At night, when human activity and traffic volumes were greatly reduced, the constraints on habitat selection by the road network were relaxed and cover type drove habitat selection, with the influence of roads a secondary consideration. The stronger avoidance during the day, when traffic rates are much higher, and support for RSF models with variable and increasing weight for roads with higher speed limits and traffic volumes, shows that the strength of road avoidance was positively correlated with disturbance intensity. The variable response in relation to risk intensity is consistent with the risk-disturbance hypothesis purported by Frid and Dill (2002).

Movements, activity levels, and concealment cover near roads were factors that most affected seasonal differences in the influence of roads on moose habitat selection. During fall, when the rut drives moose behavior, moose showed lower daytime avoidance of roads and crossed major roads more readily than during summer or winter. In winter, when moose attempt to conserve energy reserves, moose greatly reduced their activity levels and movement rates in response to both metabolic constraints imposed by the low nutritional quality of their diet

(Schwartz and Renecker 2007, Wattles and DeStefano 2013b) and restrictions on mobility

caused by deep or crusted snow (Cody 1974). At this time, the energy expenditure required to

move between cover types close to and away from roads made those movements prohibitive.

Consequently, the daytime avoidance of roads drove both diurnal and nocturnal habitat selection

in winter. These energetic constraints were not present during summer and fall, and moose

altered their habitat selection patterns in response to the change in disturbance intensity at night

versus during the day. Additionally, the greater avoidance of even class 6 roads in winter may be

linked to greater visibility and a resultant greater sense of vulnerability during the winter. A

moose that was essentially invisible in the understory next to roads during the growing season

would be visible much further from roads in winter. The result of this was that the amount of

suitable habitat for moose in winter was greatly reduced compared to during the growing season.

Animals are often forced to make choices in habitat selection in response to

environmental factors that influence energy balance and survival. These choices often contain

trade-offs in terms of costs and benefits: e.g., increased cover for better thermoregulation

coupled with reduced forage quality, or increased forage quality but increased risk of predation

(Lima and Dill 1990, Frid and Dill 2002, Creel et al. 2005). It thus follows that the choices

animals make can provide insights into the roles of environmental factors in determining fitness

for the individual. Rettie and Messier (2000) suggested that the scale (2nd order versus 3rd order;

Johnson 1980) of these influences is related directly to the strength of the influence of the factor

on fitness. Additionally, the limiting factors should continue to influence behavior until their

influence becomes less than the next most important limiting factor.

Moose avoidance of roads at both the home range and within home range scales is an

indication that roads have an influence on moose fitness. However, the energetic costs associated

with moose road avoidance may have been minimal unless moose were denied access to resources because of road avoidance. If, however, they could obtain the same resources further from roads, but decreased the risk of being killed in a vehicle collision and reduced other negative impacts from roads (e.g., stress, vigilance), the only cost would be the energy expended to move away from the road. In winter, when moose avoided roads both during the day and at night and the costs associated with moving back and forth were high, there was a greater chance of there being an overall negative consequence to avoiding roads, as resources are not as plentiful and road avoidance essentially reduced the amount of suitable habitat available to moose. The choice of whether to use habitat close to roads is similar to the decision of whether or not to cross roads. Is the risk of a vehicle collision worth access to habitat patches available on the other side of the road?

The results of the correlated random walk analysis showed that moose movements across the landscape were restricted by roads, and that movements among habitat patches were lower than expected based on the null models. However, compared to RSF analyses, there was a less obvious difference in the road-crossing rate in relation to disturbance intensity (i.e., traffic volume). Class 6 roads (i.e., lowest levels of traffic) were an exception to this, in that moose crossed these roads as predicted. Among roads with higher traffic volume (classes 2-5) there was slightly stronger avoidance of crossing roads with higher disturbance levels, but the difference was not as clear.

Most roads in Massachusetts did not serve as complete barriers to movements as moose crossed roads of all classes. However, in several instances class 2 and 3 roads did serve as boundaries to moose home ranges (Fig. 9); in general, moose crossed these roads very infrequently and the roads themselves appeared to act as home range boundaries. This was

consistent with the avoidances of roads at the home range scale reported in Wattles and

DeStefano (2013b). Interstate highways (class 1) roads were not located in or immediately

adjacent to any moose home ranges in this study. This is primarily due to moose capture

locations not being in close proximity to these roads and not necessarily a sign of a detectable

avoidance by any of our study animals. However, given the extreme traffic volumes, speeds of

travel, vehicle noise, and disproportionately high rate of moose-vehicle collisions on interstate

highways compared to even state highways in Massachusetts (Wattles 2014; chapter 2), we

expected that they may serve as strong barriers to movement.

The high density of roads and high levels of fragmentation of the landscape in

Massachusetts may force moose to cross roads that they would otherwise avoid. With very few

exceptions, individual habitat blocks are not large enough to encompass an entire moose home

range. State highways and high traffic roads bisect the landscape at a coarse scale, creating large

blocks of habitat (Fig. 1). Typical moose home ranges consist of several of these larger blocks,

with local, normally class 4, through-roads further fragmenting the larger blocks into smaller

patches. As a result, in order to avoid higher-class roads, moose have no choice but to cross these

local through-roads. This may be the reason we observed no difference in the crossing rate of

class 4 roads by real versus simulated moose during summer, and is an indication that the

magnitude of disturbance influenced crossing rate as well as habitat selection. Conversely,

despite being relatively low traffic volume roads, moose avoided crossing class 5 roads to a

greater extent. Moose may be able to avoid crossing these roads by moving around them, as they

typically bisect smaller portions of the landscape.

The results of our habitat selection analysis can be used to predict the relative probability

of selection of habitat patches (Fig. 6-8). However, these predictions represent the suitability of

the patches taken in isolation from the overall landscape, are based only on the roads out to the scale of the analysis, and do not incorporate the likelihood of moose crossing roads to reach the patches. To determine how likely a patch is to be used, one would need to combine the results of the RSF modeling, the avoidance of road crossings indicated by the CRW analysis, and a cumulative effect of the fragmentation of an area. Our analysis did not specifically address the likelihood that moose would cross multiple roads to move between habitat blocks. However, given the evident reluctance to cross roads, it seems that moose would be less likely to traverse multiple roads and areas of high road density to access isolated habitat patches. Additionally, areas of higher fragmentation would represent less desirable areas at a home range scale, despite relatively high probability of selection of individual patches.

In highly developed landscapes, facilitating wildlife movements among habitat patches is essential for conserving wildlife populations. Highway crossing structures have proven effective in assisting wildlife movements in places like the Trans Canada Highway between Banff and Jasper National Parks (Clevenger and Waltho 2000), where a single highway bisects intact habitat and multiple crossing structures have been built. However, in more developed landscapes achieving those levels of connectivity are extremely difficult. Nevertheless, even in highly developed areas, road crossing structures and underpasses have been shown to facilitate highway crossings and improve linkages on the landscape where they exist (Foster and Humphrey 1995, Poessel et al. 2014).

3.7 Management Implications

Habitat fragmentation caused by roads, as well as direct road effects, can influence how animals perceive and use a landscape. Understanding how road networks influence animal movements and habitat selection is essential for conservation planning in order to facilitate

animal movements, maintain landscape connectivity, and the availability of suitable habitat in increasingly human dominated landscapes.

Urban sprawl and expanding road networks can have multiple negative impacts on animal movements and habitat selection by reducing landscape connectivity and the availability of suitable habitat. Attempts should be made to concentrate future development in already developed portions of the landscape and to limit further development in areas that separate larger blocks of contiguous habitat. New roads and developments in existing habitat blocks greatly reduce the amount of suitable habitat available to wildlife and have impacts that extend beyond the footprint of the development. Road and development avoidance may functionally eliminate blocks as suitable habitat if edge effects of the new road(s) merge with edge effects of roads bounding the block. Furthermore, new developments that provide a new link between existing roads may have a greater impact than cul-de-sacs, as they will serve as a new through-road with greater traffic volume. Infrastructure planners should also consider the impact of the "improvement" of unpaved or narrow local through roads. Moose displayed a greater willingness to cross local through-roads than major local arteries and state highways when moving about their home ranges. Widening or paving will likely increase speeds and traffic volumes, potentially increasing the negative effects of the roadway as well as habitat fragmentation. Where possible, highway crossing structures or underpasses that facilitate animal movements should be included in new road and highway projects and incorporated into improvements and upgrades of existing highways and bridges.

Tables

Table 3.1 Frequency (number of days between road crossings) of road crossings by collared moose and simulated movement paths (CRW) for summer, fall, and winter.

Class	Moose				CRW		
	mean	min	max		mean	min	max
			Summer				
2	13.58	4.61	NEVER		5.5	2.0	142.9
3	27.84	5.32	NEVER		8.2	3.0	500.0
4	3.66	0.70	NEVER		2.7	1.0	27.8
5	9.60	2.42	NEVER		3.6	1.1	76.9
6	1.21	0.56	12.50		1.4	0.6	5.0
			Fall				
2	12.98	2.75	NEVER		5.0	1.7	500.0
3	20.60	6.10	NEVER		9.4	3.2	58.8
4	3.64	1.20	NEVER		2.1	0.7	550.0
5	4.61	1.06	NEVER		2.5	0.7	74.5
6	0.92	0.27	30.30		1.0	0.3	3.4
			Winter				
2	35.86	9.80	NEVER		9.1	4.1	55.6
3	57.94	8.13	NEVER		12.3	5.5	752.4
4	12.04	2.23	NEVER		3.6	1.3	250.0
5	19.83	2.63	NEVER		5.8	1.1	142.9
6	2.59	0.72	32.26		2.0	0.7	9.6

Table 3.2 Model coefficients (β) and standard errors (SE) for best models comparing the road-crossing rate of class 2 to 6 roads in winter, summer, and fall, of real and simulated moose in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011.

	class 2		class 3		class 4		class 5		class 6	
	β	SE	β	SE	B	SE	β	SE	β	SE
Winter									[a]	
Intercept	-0.018	0.019	0.005	0.016	-0.036	0.028	0.024	0.032	-0.014	0.106
road density	0.873	0.124	0.810	0.144	0.949	0.073	0.681	0.092	0.768	0.153
moose	0.023	0.018	-0.016	0.018	0.015	0.040	0.000	0.025	-0.058	0.024
density*moose	-0.721	0.119	-0.517	0.164	-0.632	0.102	-0.538	0.084		
Summer			[b]							
Intercept	0.062	0.019	-0.005	0.044	-0.048	0.105	-0.004	0.033	0.172	0.133
road density	0.720	0.092	1.194	0.371	0.776	0.154	1.179	0.101	0.869	0.185
moose	-0.027	0.025	0.040	0.041			-0.015	0.031		
density*moose	-0.492	0.119	-0.527	0.430			-0.671	0.103		
Fall	[c]		[d]							

	Coef	SE	Coef	SE	Coef	SE	Coef	SE	Coef	SE
Intercept	0.068	0.052	-0.017	0.036	0.026	0.079	-0.053	0.107	0.360	0.204
road density	0.869	0.419	1.772	0.416	1.577	0.218	1.667	0.287	0.956	0.285
moose	-0.102	0.033	-0.041	0.008	-0.030	0.065	0.003	0.070		
density*moose	-0.159	0.117			-0.624	0.179	-0.702	0.203		

[a] Coefficients and SE based on model averaging of m2 and m3 (final w = 0.506 and 0.494, respectively)

[b] Coefficients and SE based on model averaging of m1 and m2 (final w = 0.601 and 0.399, respectively)

[c] Coefficients and SE based on model averaging of m1 and m2 (final w = 0.307 and 0.693, respectively)

[d] Coefficients and SE based on model averaging of m2 and m3 (final w = 0.697 and 0.303, respectively)

Table 3.3 Comparison of candidate models predicting the road-crossing rate of class 2 to 6 roads by real and simulated moose for all season-class combinations in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011. Model structure for m1 = Road density + Moose + Density * Moose, m2 = Road density + Moose, and m3 = Road density, all models included a random intercept for individual moose to pair the actual and simulated crossing rates for each moose. Included are the difference in Akaike information criteria for small sample sizes (AICcΔ), AIC weight (*w*), and Model Rank.

	class 2			class 3			class4			class5			class 6		
	AICcΔ	*w*	rank	AICcΔ	*w*	rank	AICcΔ	*w*	rank	AICcΔ	*w*	rank	AICcΔ	*w*	rank
Winter															
m1	0	1	1	0	0.716	1	0	1	1	0	1	1	4.6	0.049	3
m2	21.2	<0.001	2	1.9	0.284	2	23.3	<0.001	2	21.2	<0.001	2	0	0.481	1
m3													0	0.470	2
Summer															
m1	0	0.983	1	0	0.601	1	6	0.036	3	0	1	1	7.3	0.023	3
m2	8.2	0.017	2	0.8	0.399	2	2	0.256	2	21	<0.001	2	4.3	0.103	2
m3							0	0.708	1				0	0.874	1
Fall															

m1	1.6	0.306	2	9	0.008	3	0	0.929	1	0	0.920	1	7	0.026	3
m2	0	0.693	1	0	0.691	1	5.2	0.071	2	4.9	0.081	2	4.4	0.098	2
m3	13	0.001	3	1.7	0.301	2							0	0.876	1

Table 3.4 Comparison of candidate RSF models used to predict habitat selection of moose in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011. Included are the difference in Akaike information criteria (AICΔ), AIC weight (w), and Model Rank. The habitat only model included a random intercept for individual; all other models included a random intercept for individual and a random slope for roads.

	Summer			Fall			Winter		
	ΔAIC	w	Rank	ΔAIC	w	Rank	ΔAIC	w	Rank
Day									
Road * Habitat	0	1	1	0	1	1	0	1	1
Road + Habitat	144.2	<0.001	2	40.2	<0.001	2	57.4	<0.001	2
Road	3104.7	<0.001	3	1915.5	<0.001	3	2041.7	<0.001	3
Habitat	4032.8	<0.001	4	3065.5	<0.001	4	6753.7	<0.001	4
Night									
Road * Habitat	0	1	1	0	1	1	0	1	1
Road + Habitat	72.4	<0.001	2	58.1	<0.001	2	52.6	<0.001	2
Road	5334.4	<0.001	4	4435.9	<0.001	4	3288	<0.001	3
Habitat	2518.3	<0.001	3	3084.5	<0.001	3	7557.1	<0.001	4

Table 3.5 Model coefficients (β) and standard errors (SE) for final resource selection functions modeling on seasonal day and night time moose habitat selection in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011.

Parameter	Summer		Fall		Winter	
	β	SE	β	SE	β	SE
Day						
Intercept	-0.220	0.156	-0.911	0.151	-0.004	0.140
Con	0.157	0.045	-0.006	0.064	0.723	0.041
Mix	-0.268	0.044	-0.403	0.061	0.457	0.039
Other	-1.858	0.241	-1.597	0.409	-1.644	0.271
Reg	0.613	0.040	0.706	0.053	0.830	0.039
WO	-0.096	0.067	-0.079	0.088	-0.939	0.081
WW	1.259	0.048	1.331	0.063	0.811	0.049
Road	-24.732	4.657	-28.059	5.007	-24.337	3.598
Con * Road	0.527	0.980	2.707	1.627	-0.565	0.981
Mix * Road	1.615	0.943	2.173	1.632	-0.868	0.939
Other * Road	-2.124	1.603	-7.611	5.446	-2.700	2.026
Reg * Road	5.649	0.879	-1.181	1.466	3.754	0.913
WO * Road	9.541	1.139	9.138	1.805	2.958	1.513
WW * Road	2.668	0.982	1.949	1.540	0.917	1.073
Night						
Intercept	-0.799	0.180	-1.257	0.181	0.126	0.147
Con	-0.506	0.074	-0.443	0.088	0.720	0.040
Mix	-0.649	0.068	-0.629	0.081	0.517	0.038

Other	0.384	0.159	0.775	0.195	-0.857	0.185
Reg	1.332	0.054	1.789	0.062	1.235	0.038
WO	0.812	0.081	1.099	0.088	-0.722	0.074
WW	0.870	0.072	1.223	0.080	0.655	0.048
Road	-19.070	5.172	-24.772	5.254	-25.630	6.047
Con * Road	1.948	1.474	2.162	1.998	-0.904	0.937
Mix * Road	1.835	1.411	0.299	1.975	0.787	0.871
Other * Road	-5.729	1.876	-11.620	2.803	-2.000	1.477
Reg * Road	5.692	1.166	-4.152	1.532	3.626	0.864
WO * Road	5.043	1.495	4.990	1.897	2.032	1.440
WW * Road	0.079	1.445	-1.270	1.803	0.113	1.037

Table 3.6 Final weights assigned to five roads classes (class 2, 3, 4, 5, and 6, respectively) and the scale (smoothing parameter – h (m)) used to create kernel density surfaces representing the road effect on seasonal day and night time moose habitat selection in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011.

	Weights	Scale
Day		
Summer	100 - 85- 65 - 40 - 5	500
Fall	100 - 85 - 60 - 40 - 0	1000
Winter	100 - 80 - 60 - 40 - 20	500
Night		
Summer	100 - 85 - 60 - 40 - 0	1500
Fall	100 - 85 - 60 - 40 - 0	1500
Winter	100 - 80 - 60 - 40 - 20	500

Figures

Figure 3.1 The road network (top) and estimated average daily traffic (ADT) on the road network in Massachusetts, USA.
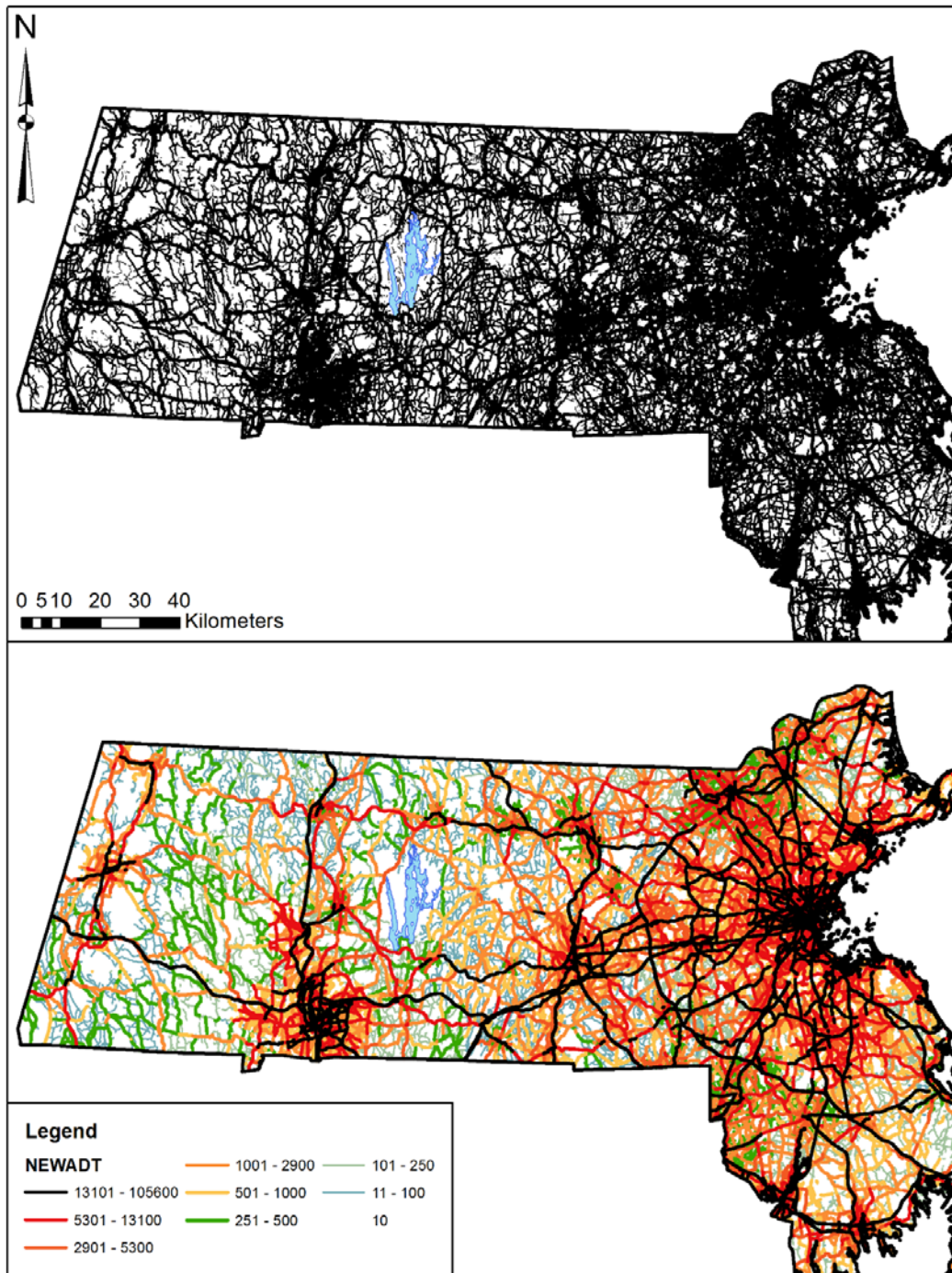
Figure 3.2 Comparison of road crossing rates versus road density (km/km2) in winter by real and simulated (correlated random walk (CRW)) moose in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011. Real moose are represented by triangles and a dashed line, simulated moose with circles and a solid line.
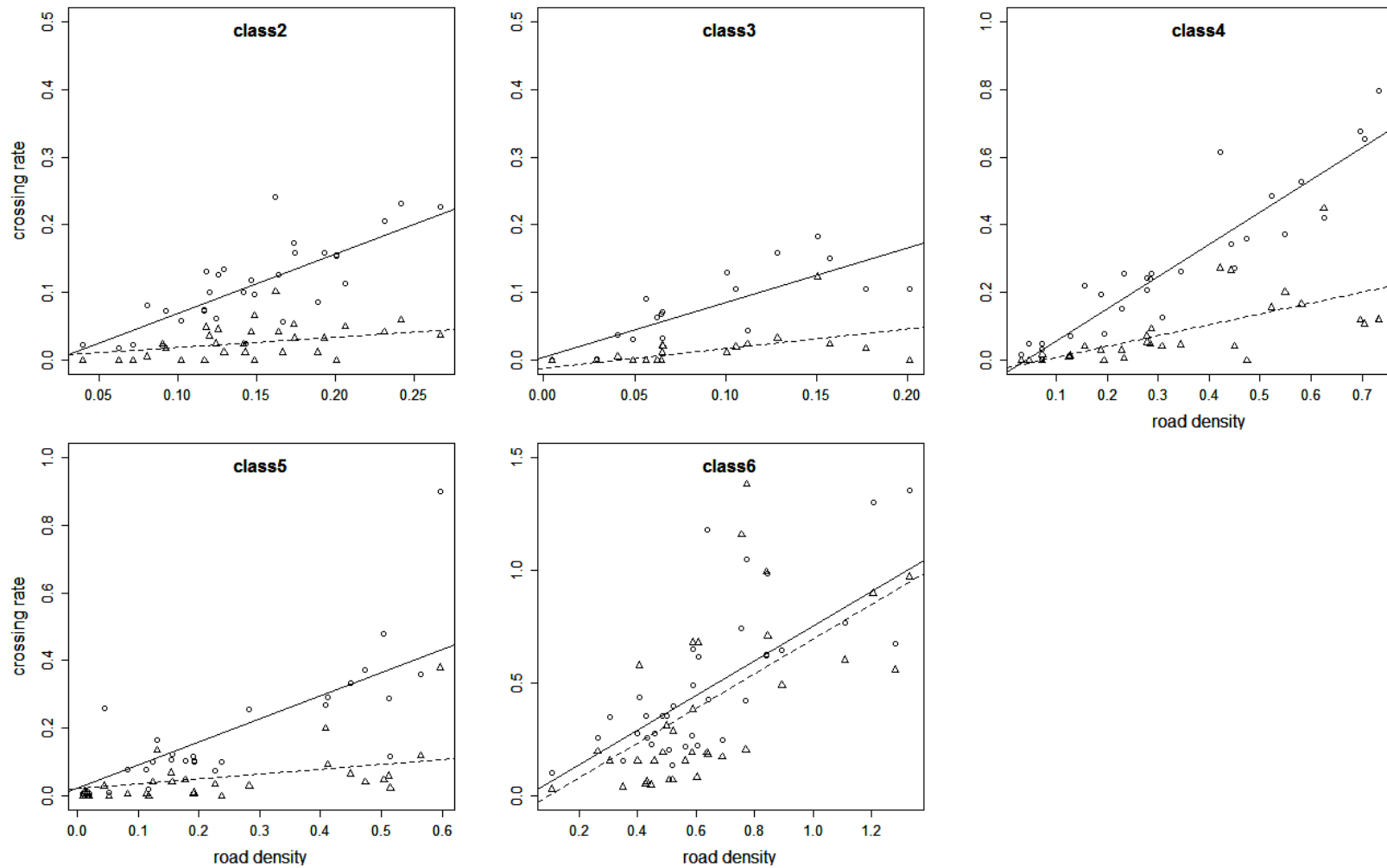
Figure 3.3 Comparison of road crossing rates versus road density (km/km2) in summer by real and simulated (correlated random walk (CRW)) moose in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011. Real moose are represented by triangles and a dashed line, simulated moose with circles and a solid line.
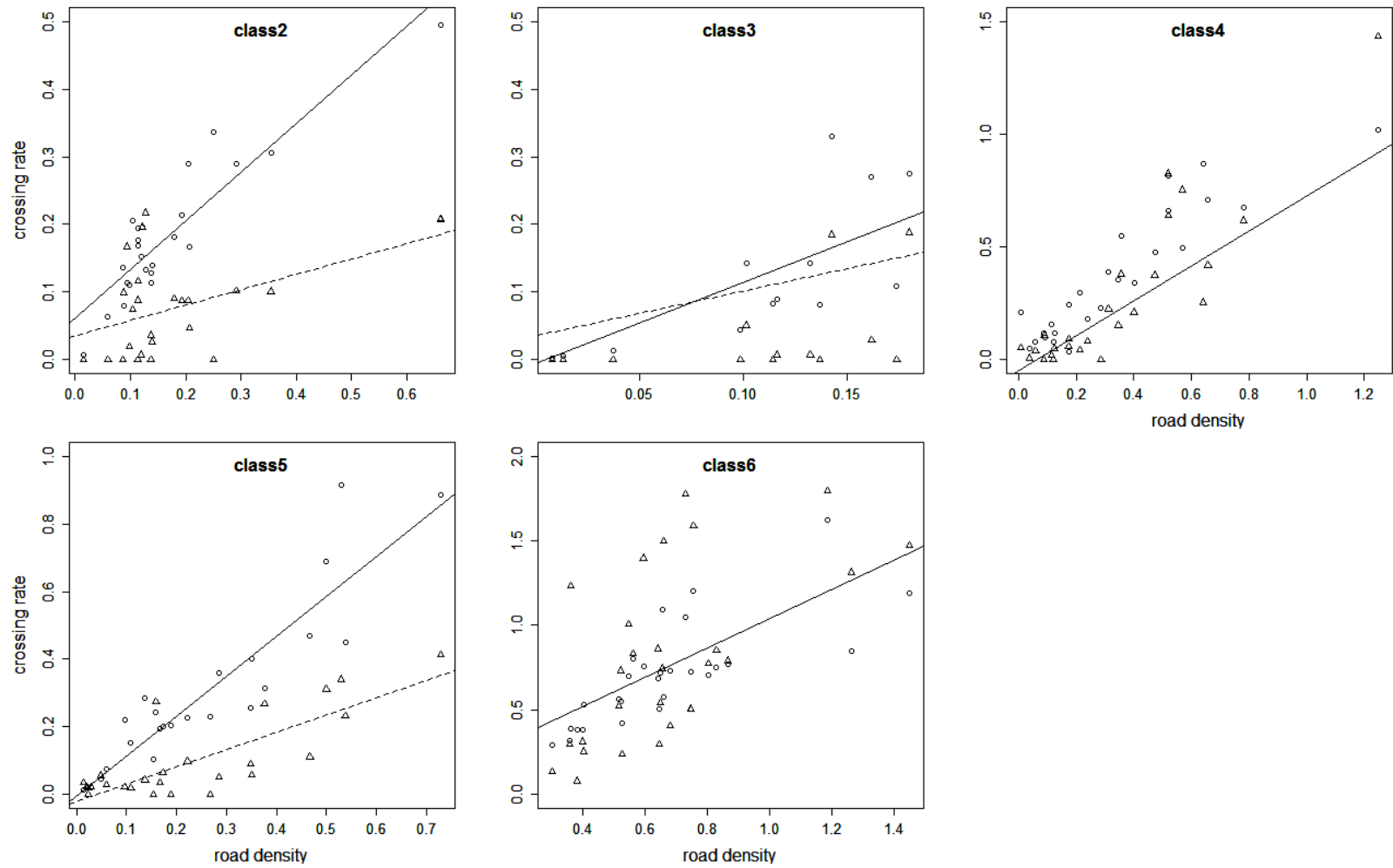
Figure 3.4 Comparison of road crossing rates versus road density (km/km2) in fall by real and simulated (correlated random walk (CRW)) moose in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011.. Real moose are represented by triangles and a dashed line, simulated moose with circles and a solid line.
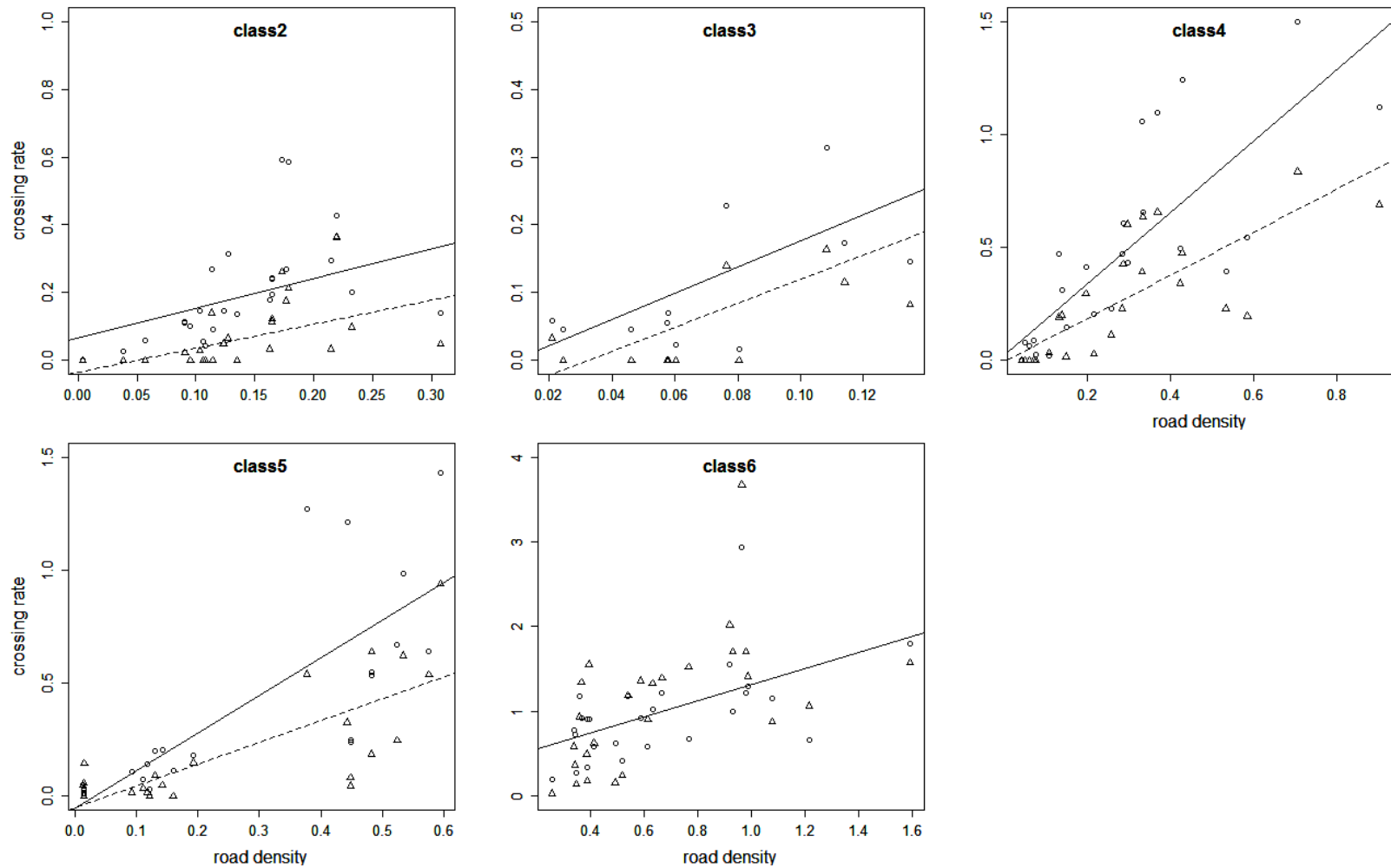
Figure 3.5 Mean (+/- standard error) length of movement steps when moose crossing roads of class 2 to 6 compared to the mean and 95th quantile of all seasonal movements including road crossings by moose in Massachusetts, USA and adjacent parts of Vermont and New Hampshire, from 2006 to 2011.
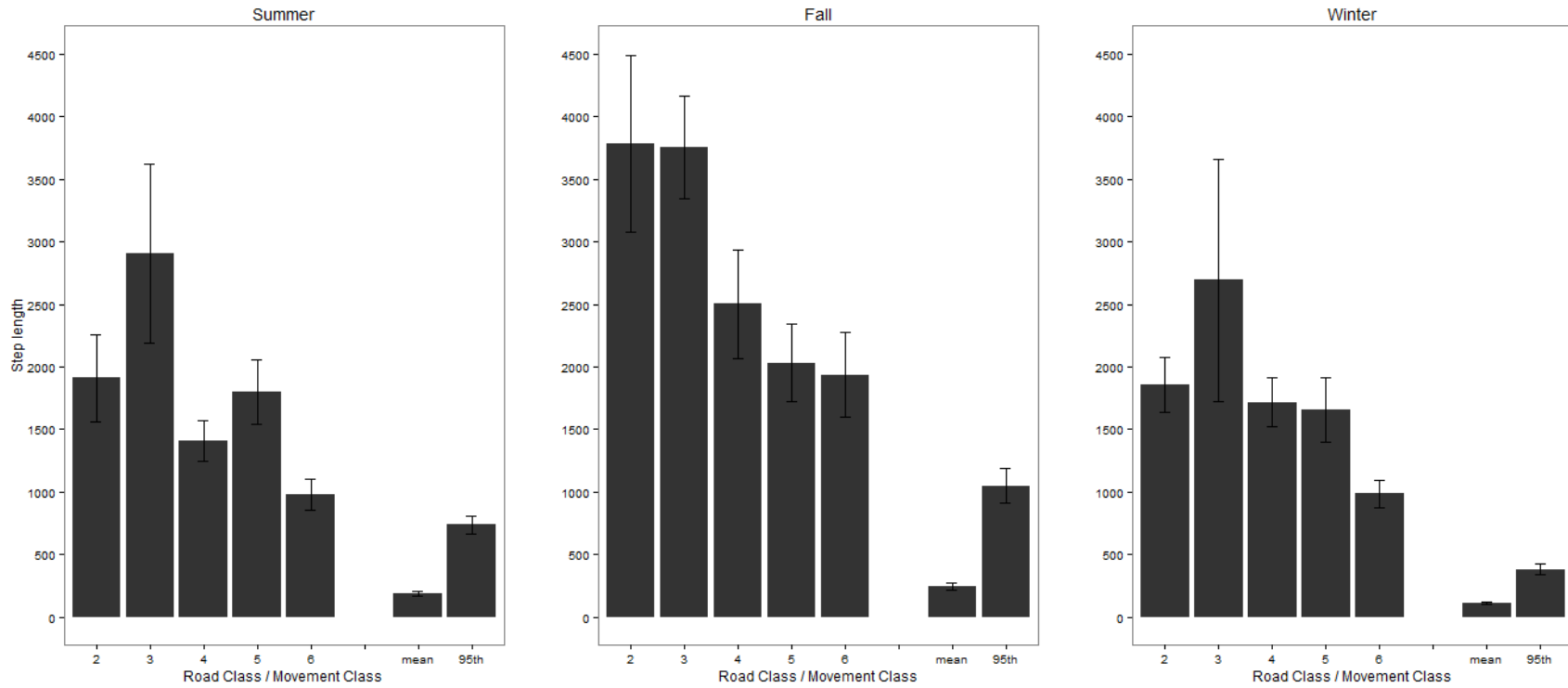
Figure 3.6 The relative probability of selection of the landscape in Massachusetts relative to the road network during the day in summer based on the results of the Road only model for that period. Black rectangle represents the enlarged area depicted in Figures 3.7 and 3.8 for comparison of seasonal and diel patterns of selection relative to roads.
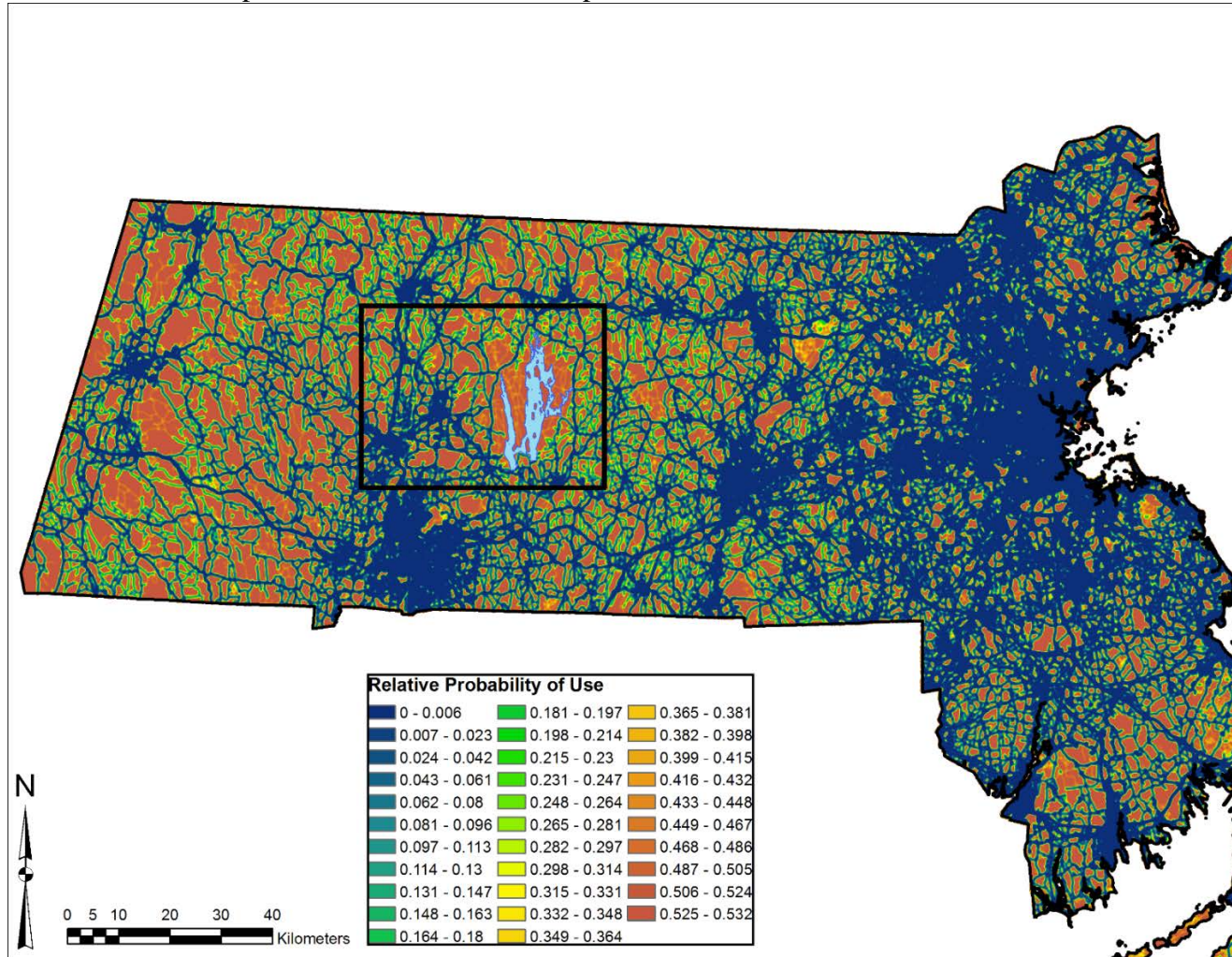
Figure 3.7 The road network (upper right; heavy lines are state highways, solid lines are public roads, and dashed lines forest roads) and seasonal daytime relative probability of use based on Road only resource selection functions for summer (upper right), fall (lower left), and winter (lower right).
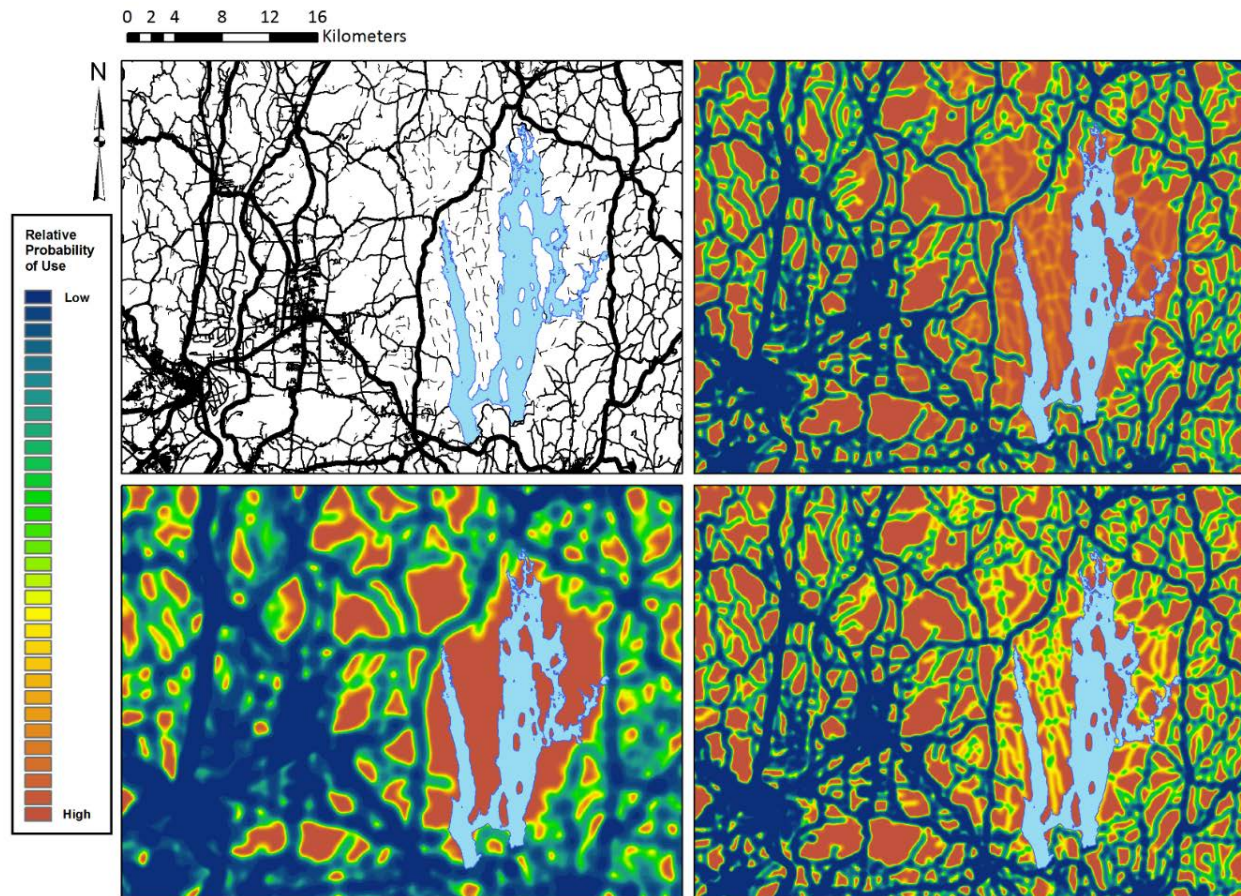
Figure 3.8 The road network (upper right; heavy lines are state highways, solid lines are public roads, and dashed lines forest roads) and seasonal nighttime relative probability of use based on Road only resource selection functions for summer (upper right), fall (lower left), and winter (lower right).
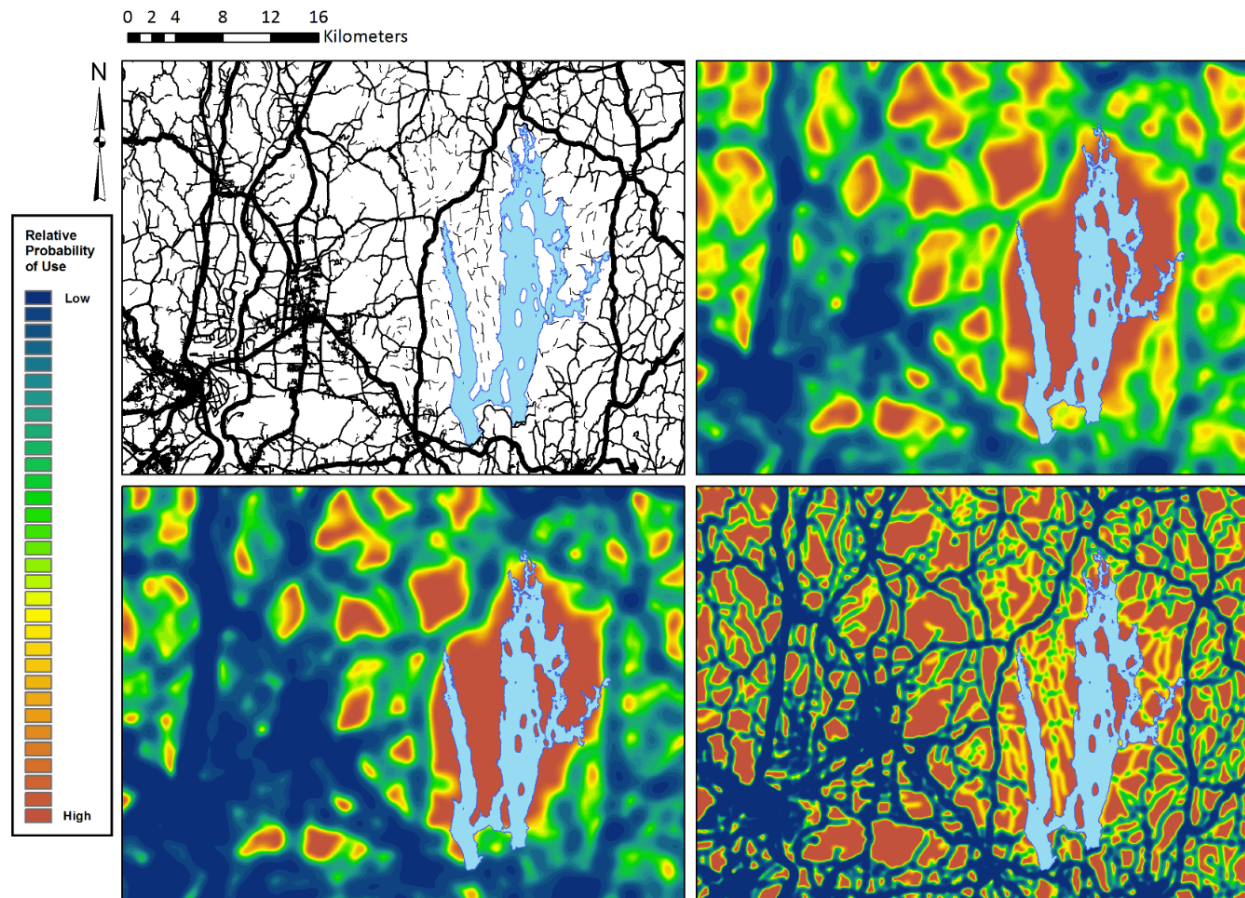
MODEL RESULTS FOR RESOURCE SELECTION FUNCTION MODELING FOR MOOSE IN CENTRAL MASSACHUSETTS. REFERENCE CATEGORY FOR COVER TYPE WAS DECIDUOUS FOREST.

Variable	Beta	SE	z-value	P-value	Variable	Beta	SE	z-value	P-value
		Spring day					Spring night		
Intercept	-3.108	0.220	-14.10	< 2e-16	Intercept	-3.485	0.204	-17.085	< 2e-16
Conifer	-0.129	0.150	-0.86	0.391	Conifer	-0.417	0.174	-2.391	0.017
Mixed	-0.343	0.153	-2.24	0.025	Mixed	-0.265	0.166	-1.599	0.110
Regen	1.460	0.132	11.06	< 2e-16	Regen	1.462	0.136	10.739	< 2e-16
Wwet	-0.206	0.159	-1.29	0.197	Wwet	-0.206	0.182	-1.132	0.258
Owet	-2.039	0.287	-7.10	0.000	Owet	-2.135	0.314	-6.797	0.000
Other	-0.962	0.362	-2.66	0.008	Other	-0.348	0.251	-1.385	0.166
AmbTemp	-0.017	0.008	-2.08	0.038	AmbTemp	-0.012	0.013	-0.949	0.343
ConiferxTemp	0.056	0.010	5.77	0.000	ConiferxTemp	0.039	0.016	2.348	0.019

MixedxTemp	0.028	0.010	2.81	0.005	MixedxTemp	0.007	0.016	0.464	0.643
RegenxTemp	-0.037	0.009	-4.15	0.000	RegenxTemp	-0.008	0.013	-0.574	0.566
WetxTemp	0.100	0.010	10.03	< 2e-16	WetxTemp	0.092	0.016	6.505	0.000
OwetxTemp	0.110	0.016	6.86	0.000	OwetxTemp	0.158	0.024	5.621	0.000
OtherxTemp	-0.067	0.029	-2.33	0.020	OtherxTemp	-0.013	0.025	-0.523	0.601
		Summer day					**Summer night**		
Intercept	-2.849	0.262	-10.88	< 2e-16	Intercept	-3.918	0.393	-9.977	< 2e-16
Conifer	-0.428	0.256	-1.67	0.094	Conifer	-0.932	0.469	-1.985	0.047
Mixed	-0.009	0.256	-0.04	0.972	Mixed	-1.543	0.526	-2.933	0.003
Regen	2.030	0.216	9.38	< 2e-16	Regen	2.532	0.367	6.892	0.000
Wwet	-0.082	0.242	-0.34	0.735	Wwet	0.067	0.419	0.161	0.872
Owet	0.271	0.273	0.99	0.321	Owet	1.018	0.411	2.481	0.013
Other	-0.550	0.954	-0.58	0.565	Other	0.893	0.500	1.787	0.074
AmbTemp	-0.003	0.010	-0.34	0.737	AmbTemp	-0.006	0.021	-0.298	0.765
ConiferxTemp	0.034	0.012	2.82	0.005	ConiferxTemp	0.059	0.028	2.148	0.032

MixedxTemp	-0.009	0.012	-0.70	0.484	MixedxTemp	0.048	0.031	1.563	0.118
RegenxTemp	-0.044	0.010	-4.31	0.000	RegenxTemp	-0.013	0.022	-0.593	0.553
WetxTemp	0.085	0.011	7.57	0.000	WetxTemp	0.093	0.025	3.782	0.000
OwetxTemp	0.030	0.013	2.38	0.017	OwetxTemp	0.063	0.024	2.574	0.010
OtherxTemp	-0.119	0.050	-2.36	0.018	OtherxTemp	-0.025	0.030	-0.829	0.407

	Fall day					Fall night			
Intercept	-3.515	0.191	-18.41	< 2e-16	Intercept	-3.730	0.183	-20.330	< 2e-16
Conifer	0.064	0.169	0.38	0.707	Conifer	-0.529	0.184	-2.873	0.004
Mixed	-0.055	0.166	-0.33	0.741	Mixed	-0.532	0.171	-3.117	0.002
Regen	1.755	0.138	12.73	< 2e-16	Regen	2.164	0.126	17.129	< 2e-16
Wwet	1.186	0.155	7.66	0.000	Wwet	1.018	0.150	6.807	0.000
Owet	0.318	0.206	1.55	0.122	Owet	0.747	0.163	4.583	0.000
Other	-0.553	0.517	-1.07	0.285	Other	0.428	0.211	2.033	0.042
AmbTemp	0.035	0.008	4.60	0.000	AmbTemp	0.029	0.010	2.928	0.003
ConiferxTemp	-0.008	0.010	-0.76	0.448	ConiferxTemp	-0.008	0.015	-0.538	0.591

MixedxTemp	-0.025	0.010	-2.50	0.012	MixedxTemp	-0.019	0.014	-1.355	0.176
RegenxTemp	-0.079	0.008	-9.40	< 2e-16	RegenxTemp	-0.050	0.010	-4.834	0.000
WetxTemp	0.012	0.009	1.35	0.176	WetxTemp	0.025	0.012	2.125	0.034
OwetxTemp	-0.015	0.012	-1.17	0.243	OwetxTemp	0.037	0.013	2.875	0.004
OtherxTemp	-0.197	0.048	-4.14	0.000	OtherxTemp	-0.104	0.020	-5.065	0.000

Early winter day					Early winter night			
Intercept	-3.102	0.184	-16.88	< 2e-16	Intercept	-2.862	0.177	-16.145	< 2e-16
Conifer	0.284	0.063	4.47	0.000	Conifer	0.101	0.057	1.761	0.078
Mixed	0.362	0.059	6.16	0.000	Mixed	0.550	0.050	10.976	< 2e-16
Regen	1.004	0.054	18.44	< 2e-16	Regen	1.448	0.046	31.260	< 2e-16
Wwet	0.701	0.070	10.06	< 2e-16	Wwet	0.782	0.058	13.429	< 2e-16
Owet	-1.204	0.146	-8.27	< 2e-16	Owet	-0.914	0.107	-8.544	< 2e-16
Other	-3.325	0.367	-9.06	< 2e-16	Other	-2.257	0.188	-11.988	< 2e-16
AmbTemp	0.018	0.007	2.44	0.015	AmbTemp	0.018	0.007	2.622	0.009
ConiferxTemp	-0.023	0.009	-2.40	0.016	ConiferxTemp	-0.051	0.009	-5.623	0.000

MixedxTemp	-0.027	0.009	-3.08	0.002	MixedxTemp	-0.033	0.008	-4.180	0.000
RegenxTemp	-0.039	0.008	-4.83	0.000	RegenxTemp	-0.020	0.007	-2.705	0.007
WetxTemp	0.059	0.010	5.24	0.000	WetxTemp	0.036	0.009	4.036	0.000
OwetxTemp	0.092	0.017	6.08	0.000	OwetxTemp	0.065	0.016	4.106	0.000
OtherxTemp	0.018	0.052	0.35	0.727	OtherxTemp	0.037	0.029	1.266	0.205

	Late winter day					Late winter night			
Intercept	-1.910	0.749	-2.55	0.011	Intercept	-2.270	0.165	-13.790	< 2e-16
Conifer	0.438	0.047	9.26	< 2e-16	Conifer	0.243	0.047	5.201	0.000
Mixed	0.285	0.045	6.27	0.000	Mixed	0.229	0.044	5.194	0.000
Regen	0.952	0.042	22.87	< 2e-16	Regen	1.061	0.040	26.453	< 2e-16
Wwet	0.452	0.055	8.23	< 2e-16	Wwet	0.220	0.054	4.055	0.000
Owet	-1.614	0.125	-12.90	< 2e-16	Owet	-1.271	0.095	-13.363	< 2e-16
Other	-2.654	0.191	-13.87	< 2e-16	Other	-1.832	0.118	-15.512	< 2e-16
AmbTemp	0.005	0.005	1.05	0.294	AmbTemp	0.032	0.005	6.178	0.000
ConiferxTemp	0.002	0.006	0.27	0.791	ConiferxTemp	-0.037	0.006	-5.881	0.000

MixedxTemp	-0.015	0.006	-2.48	0.013	MixedxTemp	-0.035	0.006	-5.756	0.000
RegenxTemp	-0.032	0.006	-5.58	0.000	RegenxTemp	-0.041	0.006	-7.392	0.000
WetxTemp	0.047	0.007	6.57	0.000	WetxTemp	0.010	0.008	1.328	0.184
OwetxTemp	0.068	0.014	4.95	0.000	OwetxTemp	0.060	0.014	4.242	0.000
OtherxTemp	0.057	0.022	2.58	0.010	OtherxTemp	0.105	0.017	6.239	0.000

APPENDIX B

MODEL RESULTS FOR RESOURCE SELECTION FUNCTION MODELING FOR MOOSE IN WESTERN MASSACHUSETTS. REFERENCE CATEGORY FOR COVER TYPE WAS DECIDUOUS FOREST.

Variable	Beta	SE	z-value	P-value	Variable	Beta	SE	z-value	P-value
		Spring day					Spring night		
Intercept	-2.037	0.189	-10.77	< 2e-16	Intercept	-2.477	0.192	-12.93	< 2e-16
Conifer	-1.539	0.142	-10.86	< 2e-16	Conifer	-2.074	0.210	-9.86	< 2e-16
Mixed	-1.291	0.121	-10.66	< 2e-16	Mixed	-0.923	0.125	-7.37	0.000
Regen	-0.304	0.104	-2.93	0.003	Regen	-0.267	0.100	-2.69	0.007
Wwet	-0.781	0.126	-6.19	0.000	Wwet	-1.455	0.175	-8.33	< 2e-16
Owet	-2.145	0.286	-7.50	0.000	Owet	-1.649	0.245	-6.74	0.000
Other	-15.595	513.127	-0.03	0.976	Other	-4.527	1.063	-4.26	0.000
AmbTemp	-0.031	0.005	-6.27	0.000	AmbTemp	-0.024	0.007	-3.53	0.000
ConiferxTemp	0.056	0.009	6.02	0.000	ConiferxTemp	0.015	0.020	0.74	0.459
MixedxTemp	0.047	0.008	5.78	0.000	MixedxTemp	-0.013	0.013	-1.04	0.301

RegenxTemp	-0.003	0.008	-0.40	0.688	RegenxTemp	0.030	0.009	3.22	0.001
WetxTemp	0.085	0.008	10.48	< 2e-16	WetxTemp	0.093	0.014	6.63	0.000
OwetxTemp	0.085	0.017	4.89	0.000	OwetxTemp	0.112	0.019	5.89	0.000
OtherxTemp	-0.560	235.484	0.00	0.998	OtherxTemp	0.081	0.082	0.99	0.324

	Summer day					Summer night			
Intercept	-1.896	0.218	-8.69	< 2e-16	Intercept	-3.537	0.318	-11.11	< 2e-16
Conifer	-1.068	0.254	-4.21	0.000	Conifer	-0.267	0.501	-0.53	0.594
Mixed	-1.023	0.247	-4.14	0.000	Mixed	-0.423	0.462	-0.92	0.360
Regen	1.319	0.201	6.56	0.000	Regen	2.374	0.308	7.72	0.000
Wwet	-0.836	0.251	-3.34	0.001	Wwet	0.667	0.419	1.59	0.111
Owet	1.830	0.290	6.31	0.000	Owet	2.778	0.359	7.74	0.000
Other	2.022	1.737	1.16	0.244	Other	-0.479	1.062	-0.45	0.652
AmbTemp	-0.018	0.009	-2.10	0.035	AmbTemp	0.010	0.018	0.56	0.575
ConiferxTemp	0.061	0.013	4.85	0.000	ConiferxTemp	-0.023	0.031	-0.75	0.453
MixedxTemp	0.045	0.012	3.69	0.000	MixedxTemp	-0.013	0.028	-0.48	0.634

	Coef.	SE	t/z	p		Coef.	SE	t/z	p
RegenxTemp	-0.020	0.010	-1.92	0.055	RegenxTemp	-0.008	0.019	-0.41	0.684
WetxTemp	0.091	0.015	7.42	0.000	WetxTemp	0.003	0.025	0.14	0.892
OwetxTemp	-0.054	0.012	-3.55	0.000	OwetxTemp	-0.042	0.022	-1.93	0.054
OtherxTemp	-0.382	0.137	-2.78	0.005	OtherxTemp	-0.039	0.065	-0.60	0.547

	Fall day					Fall night			
Intercept	-3.076	0.208	-14.81	< 2e-16	Intercept	-3.521	0.194	-18.19	< 2e-16
Conifer	0.139	0.130	1.07	0.285	Conifer	0.239	0.129	1.85	0.065
Mixed	-0.158	0.131	-1.20	0.229	Mixed	-0.134	0.131	-1.02	0.308
Regen	1.422	0.103	13.77	< 2e-16	Regen	2.073	0.096	21.54	< 2e-16
Wwet	0.098	0.133	0.73	0.465	Wwet	0.350	0.139	2.51	0.012
Owet	-0.515	0.221	-2.33	0.020	Owet	0.693	0.155	4.46	0.000
Other	-3.597	1.215	-2.96	0.003	Other	-1.300	0.379	-3.43	0.001
AmbTemp	0.013	0.007	1.89	0.059	AmbTemp	0.029	0.008	3.47	0.001
ConiferxTemp	-0.024	0.010	-2.32	0.020	ConiferxTemp	-0.055	0.013	-4.12	0.000
MixedxTemp	-0.027	0.010	-2.59	0.010	MixedxTemp	-0.047	0.013	-3.49	0.000

RegenxTemp	-0.058	0.008	-7.09	0.000	RegenxTemp	-0.045	0.009	-4.82	0.000
WetxTemp	0.065	0.009	2.14	0.000	WetxTemp	0.030	0.013	2.34	0.019
OwetxTemp	0.034	0.016	6.87	0.032	OwetxTemp	0.032	0.014	2.30	0.022
OtherxTemp	-0.029	0.096	-0.30	0.764	OtherxTemp	-0.018	0.037	-0.48	0.629

Early winter day					Early winter night			
Intercept	-2.927	0.223	-13.11	< 2e-16	Intercept	-2.549	0.222	-11.49	< 2e-16
Conifer	0.759	0.051	14.81	< 2e-16	Conifer	0.663	0.044	15.02	< 2e-16
Mixed	0.287	0.052	5.48	0.000	Mixed	0.310	0.044	6.98	0.000
Regen	0.601	0.051	11.86	< 2e-16	Regen	0.909	0.041	21.95	< 2e-16
Wwet	0.463	0.065	7.07	0.000	Wwet	0.493	0.054	9.20	< 2e-16
Owet	-0.632	0.125	-5.05	0.000	Owet	-0.097	0.081	-1.20	0.230
Other	-5.254	1.124	-4.68	0.000	Other	-4.626	0.750	-6.17	0.000
AmbTemp	0.004	0.006	0.72	0.473	AmbTemp	0.005	0.005	0.98	0.325
ConiferxTemp	-0.008	0.007	-1.02	0.307	ConiferxTemp	-0.031	0.007	-4.83	0.000

	Estimate	SE	t	p		Estimate	SE	t	p
MixedxTemp	-0.030	0.008	-4.00	0.000	MixedxTemp	-0.024	0.007	-3.58	0.000
RegenxTemp	-0.013	0.007	-1.79	0.073	RegenxTemp	0.009	0.006	1.43	0.151
WetxTemp	0.054	0.009	5.93	0.000	WetxTemp	0.011	0.008	1.42	0.157
OwetxTemp	0.106	0.016	6.76	0.000	OwetxTemp	0.085	0.012	6.90	0.000
OtherxTemp	0.046	0.155	0.30	0.767	OtherxTemp	0.207	0.103	2.01	0.045

	Late winter day					Late winter night			
Intercept	-2.422	0.210	-11.53	< 2e-16	Intercept	-2.240	0.212	-10.56	< 2e-16
Conifer	1.088	0.039	27.89	< 2e-16	Conifer	1.021	0.041	25.20	< 2e-16
Mixed	0.661	0.039	16.74	< 2e-16	Mixed	0.661	0.040	16.39	< 2e-16
Regen	0.426	0.041	10.29	< 2e-16	Regen	0.534	0.042	12.83	< 2e-16
Wwet	0.903	0.047	19.14	< 2e-16	Wwet	0.878	0.048	18.41	< 2e-16
Owet	-1.108	0.112	-9.92	< 2e-16	Owet	-1.058	0.112	-9.48	< 2e-16
Other	-5.557	1.078	-5.16	0.000	Other	-4.623	0.638	-7.24	0.000
AmbTemp	0.004	0.004	0.98	0.326	AmbTemp	0.031	0.004	7.35	0.000

ConiferxTemp	-0.032	0.005	-6.59	0.000	ConiferxTemp	-0.062	0.005	-12.28	< 2e-16
MixedxTemp	0.002	0.005	0.39	0.695	MixedxTemp	-0.018	0.005	-3.46	0.001
RegenxTemp	-0.016	0.005	-3.19	0.001	RegenxTemp	-0.034	0.005	-6.35	0.000
WetxTemp	0.046	0.005	8.63	< 2e-16	WetxTemp	0.007	0.006	1.20	0.230
OwetxTemp	-0.029	0.014	-2.06	0.040	OwetxTemp	-0.033	0.013	-2.45	0.014
OtherxTemp	0.133	0.075	1.77	0.076	OtherxTemp	0.107	0.078	1.37	0.171

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