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Original investigation

Range expansion in unfavorable environments through behavioral responses to microclimatic conditions: Moose (*Alces americanus*) as the model

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ABSTRACT

Wildlife populations occurring at the edge of their range boundaries are thought to be the most sensitive to climate change due to temperatures being at or near the limit of a species' thermal envelope. Moose (*Alces americanus*) are a cold adapted species that are showing population declines in some portions of the southern edge of their range. However, other moose populations are actively expanding southward into thermally stressful areas. The direct effects of temperature on moose have not yet been studied in these southwardly expanding populations and may offer insights into how moose are successfully establishing in areas at the edge of their thermal envelope. We used ambient temperature and GPS collar data from moose to quantify the direct effect of temperature on moose habitat use in Massachusetts, USA, which is one of these southwardly expanding populations. The mean daily temperature in our study area exceeded the reported physiological tolerances of moose in over 90% of daytime and 75% of nighttime locations in summer and in over 80% of daytime and 67% of nighttime locations in winter. Across seasons and times of day, moose preferred regenerating forest, but as ambient air temperatures increased, selection for regenerating forest declined and selection for forested wetlands and coniferous forest increased. This response indicates moose are altering their behavior to utilize thermal shelters when temperatures are high. We observed higher temperatures and stronger behavioral responses than other studies at the southern edge of moose range. We found habitat for moose in Massachusetts is climatically marginal and loss of habitat, increase in parasites, and further climatic warming may cause population declines in the future.

Introduction

Human-induced climate change is already impacting the distributions of species worldwide (Chen et al., 2011). Populations occurring at range boundaries are thought to be the most sensitive to climate change due to temperatures being at or near the limit of a species' thermal envelope (Caughley et al., 1988; Pearson and Dawson, 2003a,b). Understanding the thermal environments of species can augment our foundational understanding of what constitutes habitat (Elmore et al., 2017), and quantifying the response of populations to limiting temperatures – whether they "adapt, move, acclimate, or die" – can help natural resource managers and policy makers detect species responses to climate change and prioritize species for conservation action (Beever et al., 2017).

Moose (*Alces amercianus*) are a cold adapted species that have been shown to have increased mortality along the southern edge of their range (Lenarz et al., 2009; Monteith et al., 2015; Murray et al., 2006). This increased mortality is hypothesized to be an effect of heat stress, or hyperthermia. Due to their large body size, low surface-area to-volume ratio, and a dark, dense insulating coat, moose begin to experience hyperthermia at relatively low ambient temperatures. Experiments with captive moose (McCann et al., 2013; Renecker and Hudson, 1986) have shown exponential increases in heart rate, respiration, and metabolic rates at temperatures above -5 °C in winter and 14 °C in summer, and open-mouthed panting at temperatures above 0 °C in winter and 20 °C in summer. Heat stress at these upper critical temperatures (UTCs) can suppress appetite and reduce foraging time (Belovsky and Jordan, 1978; De Rensis and Scaramuzzi, 2003; Knorre, 1959; Renecker and Hudson, 1986; Schwab and Pitt, 1991) and has been shown to invoke behavioral responses in moose to seek out thermal shelters where the quantity and quality of forage may be relatively low (Dussault et al.,

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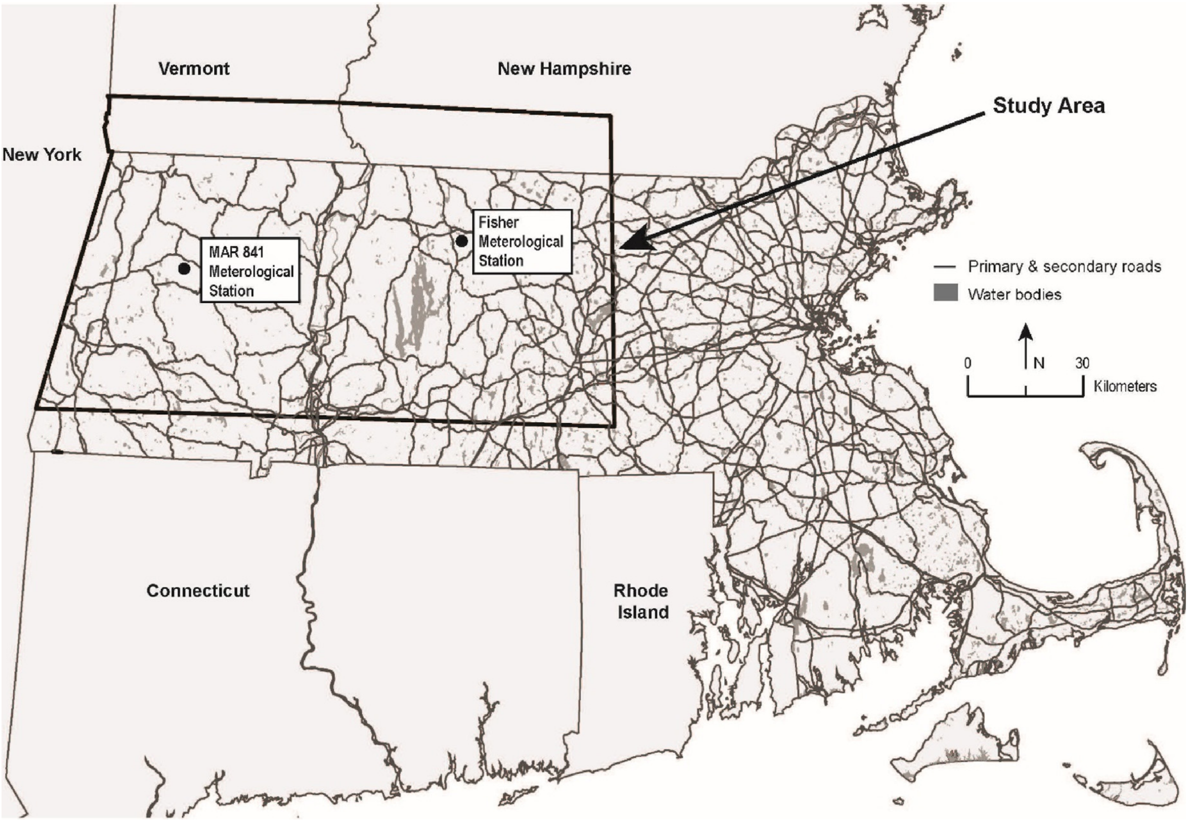

Fig. 1. Study area in west-central Massachusetts and bordering areas of adjacent Vermont and New Hampshire.

2004; van Beest et al., 2012). These responses can lead to malnutrition (Murray et al., 2006), weight loss (Renecker and Hudson, 1986), or reduced weight gain (Knorre, 1959), which can cause several indirect effects such as lower reproductive output, mortality, and susceptibility to predators, parasites, and disease (Lenarz et al., 2009; Mech and Fieberg, 2014; Monteith et al., 2015; Samuel, 2007).

The negative responses of moose to UTCs have been hypothesized to be the cause of moose population declines in Minnesota (Lenarz et al., 2009; Murray et al., 2006), Nova Scotia (Broders et al., 2012), and in Utah, Colorado, and Wyoming (Montieth et al., 2015). At the same time, moose are expanding southward into other areas that experience temperatures at or beyond moose UTCs for prolonged periods of time. For example, moose populations are moving south into Washington State (Base et al., 2006) and are recolonizing previously established range areas in southern New England (Wattles and DeStefano, 2013). The latter recolonization is especially curious since the northeastern United States has experienced a faster warming trend during the last 200 years than other areas of the country (Karmalkar and Bradley, 2017; Walsh et al., 2014). The direct effects of temperature on moose have not yet been studied in these southward expanding populations and may offer insights into how moose are successfully establishing in areas at the edge of their thermal envelope. These insights may aid in conservation and management efforts for other moose populations along the southern range boundary – especially under a changing climate.

We examine the behavior of a moose population in central and western Massachusetts, U.S.A. which has a high human population density and is at the southern edge of moose range. We combined temperature data from meteorological stations with moose GPS telemetry data to quantify (1) the thermal environment in Massachusetts across seasons, (2) the environment moose experienced in Massachusetts across seasons, and (3) moose utilization of thermal shelters in response to high temperatures. This approach should help to elucidate both the processes underlying interactions between climate change and wildlife, and how behavior, habitat configuration, and other factors may ameliorate the potential effects of climate change on wildlife populations.

Material and methods

Study area and seasons

Our study area was located in central and western Massachusetts and adjacent portions of Vermont and New Hampshire, USA, which is the southern extent of moose range in northeastern North America (Fig. 1). Elevations range from just above sea level to 850 m and topography in the uplands is dominated by glaciated hills with abundant small streams, lakes, ponds, and wetlands. Second or multiple growth mixed deciduous forest covers > 80% of the study area (Hall et al., 2002) and consists of four main types: 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; Wattles and DeStefano, 2013; Westveldt et al., 1956 for a more detailed description of forest types). Early successional forested habitats exist primarily through moderate timber harvesting (27% of forest volume) of small patches (mean size = 16.5 ha) and secondarily through wind events or beaver activity (Kittredge et al., 2003). From 1984–2000, about 1.5% of the forest in the study area was harvested annually (Kittredge et al., 2003; McDonald et al., 2006). The pattern of forest harvest and transitional forest types, as well as a history of glaciation, provides a patchy mosaic of forest types, age classes, and wetlands.

We identified four seasons based on moose movement rates and several ecological factors that could influence moose habitat selection and behavior, such as vegetation phenology (leaf out, leaf drop, dormancy), weather (including temperature and snow conditions), and the moose reproductive cycle (Appendix A). The seasons identified were: spring (16-April – 31-May), summer (1-June – 31-August), fall (1-September – 31-October), and winter (1-November – 15-April).

Moose capture and collaring

We captured 21 adult (>1 year old) moose (5 females and 16 males) by opportunistically stalking and darting them from the ground between March 2006–November 2009. Moose were fit with either ATS G2000 series GPS collars (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) or Telonics TWG-3790 GPS collars (Telonics, Inc., Mesa, Arizona, USA). We programmed the collars to acquire a GPS fix as frequently as possible while allowing the battery life to extend for at least one year. Therefore, a GPS location was attempted every 45, 75, or 135 min. Nine moose were re-collared when their initial collar batteries ran low. The fix success rate was 85% and locational error, as reported by collar manufacturers, ranged from 2 m–45 m with a mean of 30 m. We removed fixes (approximately one per individual) that were visually obvious outliers, which resulted in 127,408 locations for use in the analysis. Seasonal data for an individual was included in the analyses only if data were available from that individual for the entire season. Mean number (and standard deviation) of locations per animal was 464 (91) in spring, 677 (145) in summer, 583 (212) in fall, and 1159 (174) in winter. Research on live animals followed ASM guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists, 2016). Capture and handling procedures were approved by the University of Massachusetts Institutional Animal Care and Use Committee protocol number 25-02-15, 28-02-16, and 211-02-01.

Resource selection functions

Because available GIS land cover layers did not accurately identify forest structure and composition in the study area (e.g., deciduous versus coniferous growth and age classes), we manually classified land cover types for the moose locations using available orthoimagery (1:5000 scale), satellite imagery (1:12,000 scale), and wetland data (1:12,000 scale; (Massachusetts Office of Geographic Information 2011; National Agriculture Imagery Program 2011). Through visual examination of the imagery and first-hand knowledge of the landscape, we identified one of the following seven covariates for each moose GPS location: (1) coniferous forest, (2) deciduous forest, (3) mixed deciduous and coniferous forest, (4) regenerating forest (logged areas <20 years old and powerline right-of-ways), (5) forested wetlands (coniferous, mixed, and deciduous wetlands), (6) open wetlands (grassy fens, shrub swamps, bogs, deep wetlands, and open water), and (7) other (including areas of human development). Our eighth covariate was ambient temperature. Ambient temperature for each moose GPS location was measured from the closer of two weather stations (described below) at the time nearest to the GPS fix. All moose home ranges were located <30 km from one of these weather stations.

We constructed third-order (Johnson, 1980) resource selection functions (RSF; Manly et al. 2002), which included a random effect for each individual moose (Gillies et al., 2006), and interaction terms of temperature by cover type. We used deciduous forest as the reference cover type for all models. Using R-software (R Core Team, 2017) and the lme4 package (Bates et al., 2012), we estimated RSF coefficients with mixed-effect logistic regression models and a Laplace approximation. We created RSFs for each season and for day and night within seasons. Preliminary analyses showed no significant differences in resource use by sex, therefore sexes were combined in the models. Availability for each individual was based on a random sample of 1000 locations generated within the animal's annual minimum convex polygon. The minimum convex polygon area for female moose was 62.2 km^2 (SD 7.7 km^2) and for male moose was 88.8 km^2 (SD, 16.8 km^2; Wattles and DeStefano, 2013). We added a 1000 m buffer around each minimum convex polygon to account for available areas within the step length distribution of moose movement distances. Available locations in the buffered area were identified by randomly sampling points in the buffered area at the same density as the available points within the minimum convex polygon for each moose. This resulted in an initial available sample size for each moose of 1175–1527 points. We assigned five different temperatures to each available point by randomly drawing, with replacement, from the distribution of temperatures at the GPS locations for each moose. The different temperatures were incorporated by duplicating the available dataset five times. Therefore, each moose had between 5875 – 7635 available points for the RSF models.

We assessed the predictive ability of our models by performing a 10-fold cross validation (Boyce, 2006). We compared the predicted observations with the expected observations (Johnson et al., 2006) using Lin's (1989) concordance correlation coefficient (CCC). In addition, we compared the temporal use of cover types by calculating the proportion of GPS locations within a cover type for each hour of the day, for each season.

Ambient temperature, upper critical temperatures, and thermal shelters

We obtained ambient air temperature data every 15 min from the Fisher Meteorological Station at Harvard Forest, Petersham, Massachusetts, and the MAR 841 station in Peru, Massachusetts (Fig. 1).

Following Renecker and Hudson (1986) and McCann et al. (2013), we identified two upper critical temperatures (UCTs) for moose during summer and winter. The lower UCTs (14 °C for summer and -5 °C for winter) invoke exponential increases in respiratory, heart, and metabolic rates. The higher UTCs (20 °C for summer and 0 °C for winter) cause open-mouth thermal panting. Identifying the UTCs for spring and fall was more difficult, as moose are shedding or growing winter coats and likely experience thermal stress at temperatures between the summer and winter UCTs. Therefore, we present spring and fall temperatures relative to both summer and winter thresholds.

Based on previously published literature, we assumed forested cover types would be cooler than ambient air temperatures during the day with coniferous forest offering the coolest temperatures followed by mixed forest and deciduous forest (Demarchi and Bunnell, 1993; Edgerton and McConnell, 1976; Parker and Gillingham, 1990). We also assumed regenerating forest, which had a more open canopy than mature forest, would be hotter than ambient air temperatures during the day (Bowyer and Kie, 2009). To aid in verifying these assumptions for our study area, we deployed Thermochron i-button temperature sensors (Embedded Data Systems, Lawrenceburg, Kentucky, USA) in eight blocks of regenerating forest, mature coniferous forest, and mature deciduous forest from August 2008 to August 2009 (further details in Appendix B). We compared the maximum temperatures in each cover type with the maximum ambient air temperatures from the Fisher Meteorological Station.

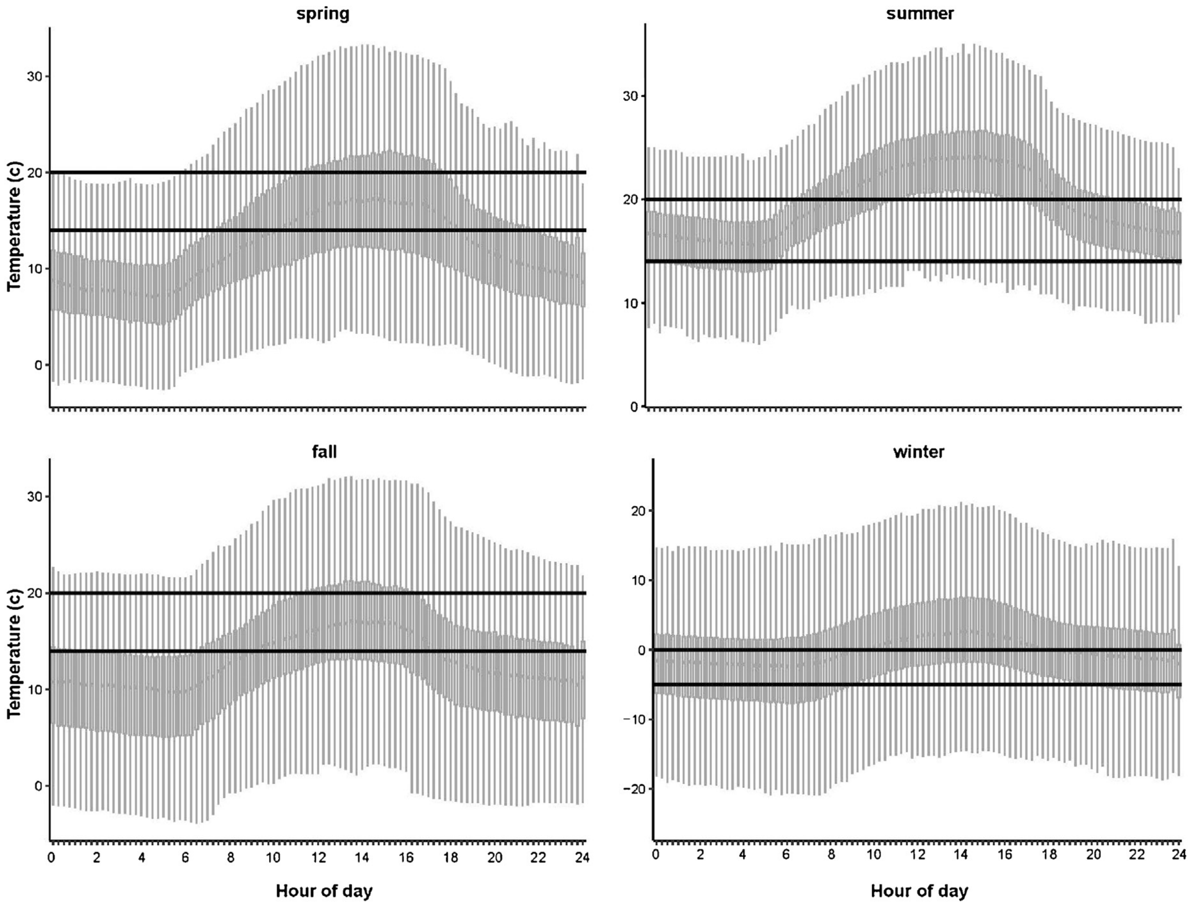

Fig. 2. Tukey's boxplots of the mean seasonal 24 h ambient temperature patterns for winter, spring, summer, and fall 2006–2011. Temperatures (°C) were recorded every 15 min at the Fisher Meterological Station, Harvard Forest, Petersham, Massachusetts. Outliers are not depicted. Horizontal lines are the seasonal upper critical temperatures. The lower temperature is when metabolic rates increase, the upper is when panting occurs (Renecker and Hudson, 1986).

Results

Ambient temperatures experienced by moose

From 2006 to 2011, daily mean temperatures at the meteorological stations exceeded the lower UCTs on 87% (316 days ± 4; $\bar{X}$ ± SE) or 68% (248 days ± 4) of the days of the year, when -5 °C or 14 °C were used for spring and fall, respectively. Daily maximum temperature exceeded these UCTs on 96% (352 days ± 2) or 89% (326 days ± 2) of the days of the year. When the maximum daily temperature exceeded the lower UCT, it did so by an average of 7.4 °C ± 0.3, 11.2 °C ± 0.2, 6.2 °C ± 0.2, and 11.3 °C + 0.3 from spring to winter, respectively. Daily minimum temperatures exceeded the lower UCTs on 68% (249.1 days + 6.2) or 42% (152.5 days + 6.6) of days of the year; on these days ambient temperature was never within the thermal neutral zone of moose. Each summer there were at least two periods with a mean duration of 13 days when temperatures did not fall below the 14 °C UCT for a week or more. On two occasions, the daily minimum temperature stayed above the 14 °C UCT for over 22 days. Throughout the year, ambient temperatures regularly exceeded the UCTs for the majority of daylight hours (Fig. 2). Upper critical temperatures were exceeded more frequently in summer and winter than in spring and fall, and typically did so for longer periods and by a greater magnitude.

Data from collared moose in the study area indicated moose were exposed to temperatures that were consistently outside of their thermal neutral zone in all seasons both day and night (Table 1). 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 winter, temperatures were above the −5 °C threshold for 80% of daytime locations and 67% of nighttime locations.

Table 1
Percent of moose GPS locations (and standard deviations) recorded when ambient temperatures exceeded seasonal upper critical temperatures. Temperatures of −5 and 14 °C result in increased metabolic rates and temperatures of 0 and 20 °C result in thermal panting for winter and summer respectively (Renecker and Hudson, 1986).

Ambient temperature	Spring		
	Day	Night	Total
>14°C UCT	47 (4)	20 (4)	36 (3)
>20°C UCT	18 (3)	2 (1)	11 (2)
Ambient temperature	Summer		
	Day	Night	Total
>14°C UCT	89 (3)	72 (5)	83 (4)
>20°C UCT	51 (7)	14 (4)	36 (5)
Ambient temperature	Fall		
	Day	Night	Total
>14°C UCT	46 (16)	21 (10)	33 (12)
>20°C UCT	14 (8)	3 (2)	8 (5)
Ambient temperature	Winter		
	Day	Night	Total
>−5°C UCT	77 (6)	64 (7)	70 (6)
>0°C UCT	51 (7)	34 (6)	41 (6)

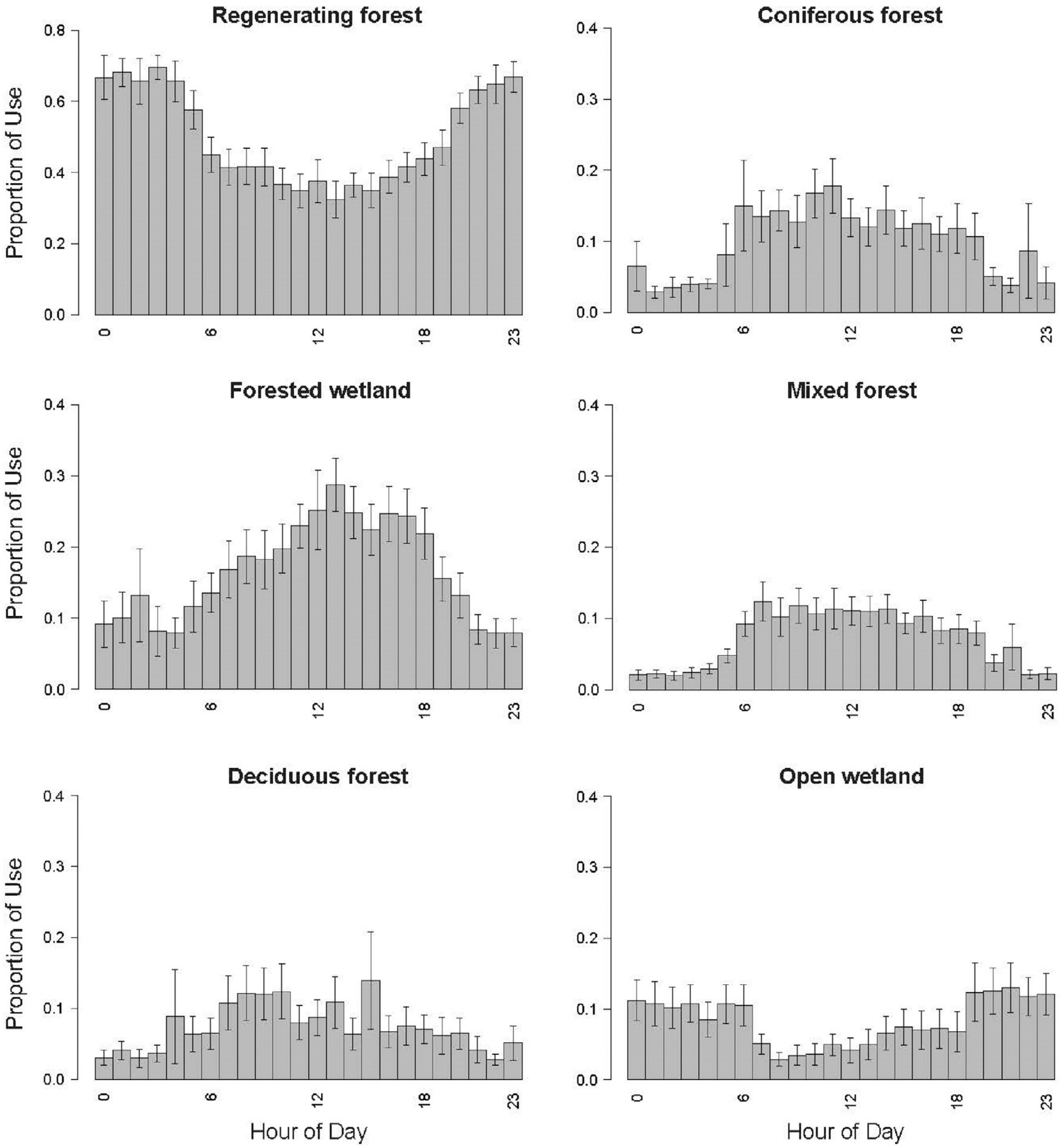

Fig. 3. Hourly proportional use of vegetation cover types (± standard error) by moose in summer in Massachusetts, USA. Note that the scale for regeneration cover type is 0–0.8 while the scale for all other cover types is 0–0.4. Hourly proportional use plot for fall, winter, and spring are provided in Appendix C.

From our temperature sensor data, we found coniferous forest types to be consistently cooler than the maximum ambient air temperature and regenerating forest to be consistently warmer than the maximum ambient air temperature across all seasons (Appendix B). We found temperatures in deciduous forests to closely match the maximum ambient air temperature in the spring and be slightly less than the maximum ambient air temperature during other times of the year (Appendix B). We were unable to place temperature sensors in wetland cover types, however, given the findings of Belovsky (1981), Ackerman (1987), Renecker and Hudson (1990) and Cosenza et al. (2003) on the capacity of water to cool moose, we assumed forested wetlands would offer the greatest shelter to moose from high temperatures.

Resource selection by moose

Across all seasons and times of day, moose used regenerating forest more than other cover types, but during the day, moose reduced their use of regenerating forest and showed a corresponding increase in use of thermal refuges, such as forested wetland and coniferous forest (Fig. 3; Appendix C). Use of regenerating forest was 48%, 55%, and 64% greater at night than during the day and use of forested wetlands was 93%, 123%, and 83% greater during the day than at night during spring, summer, and fall, respectively.

We observed these same trends in our resource selection functions. In all seasons and times of day, moose preferred regenerating forest, but as ambient air temperatures increased, selection for regenerating forest declined (Fig. 4; model coefficients are provided in Appendix D). This decline was more pronounced during the day than at night. Conversely, relative selection for forested wetlands increased with increasing temperature during both day and night (Fig. 4; Appendix D). Selection for coniferous forest and open wetlands also increased with temperature, but to a lesser extent than forested wetlands (Fig. 4; Appendix D). At night in winter, selection for regeneration remained high, even at seasonally high temperatures and decreased less with increasing temperature than

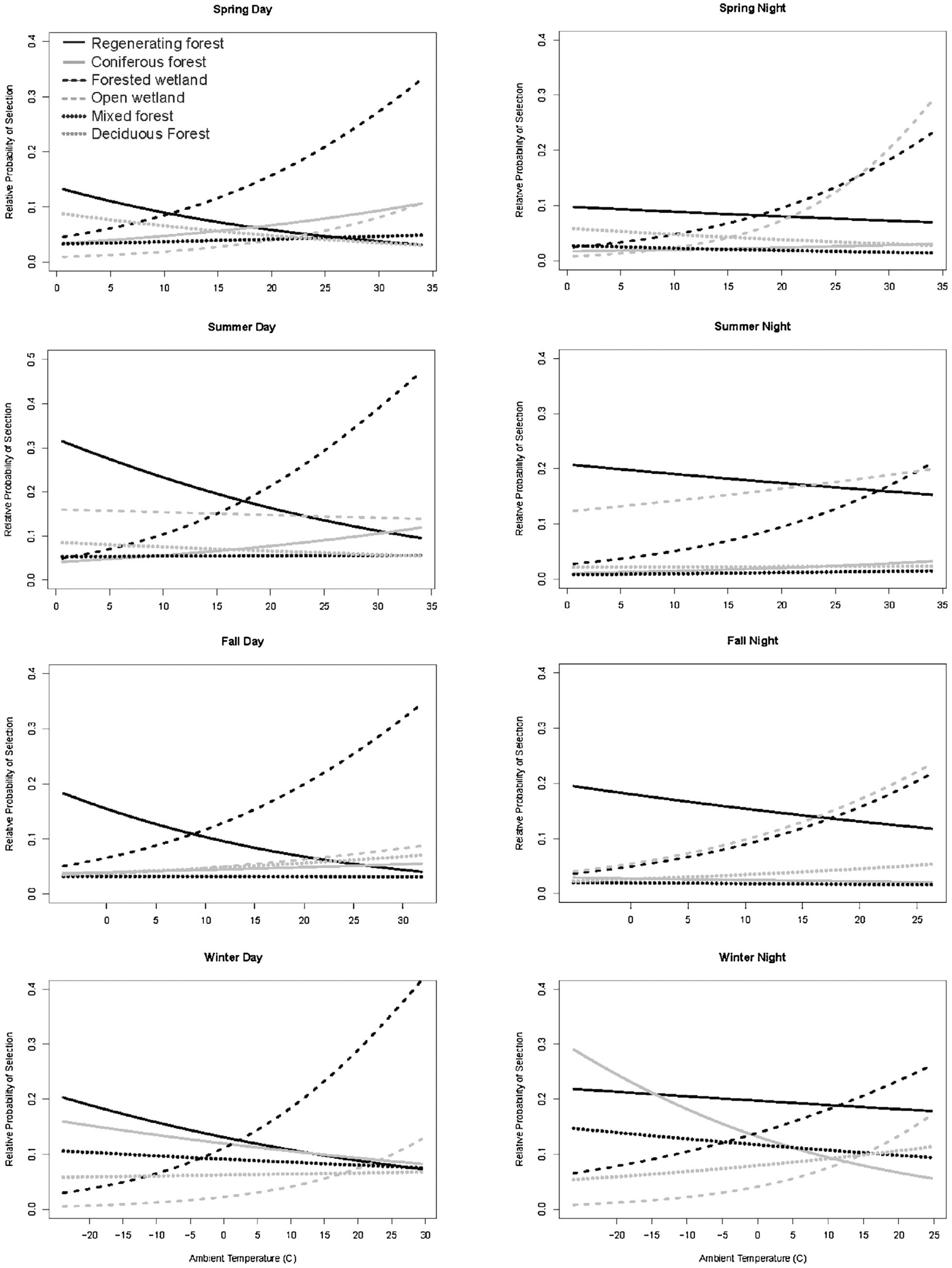

Fig. 4. Relative probability of selection of cover types by moose as a function of ambient temperature for day and night models during spring, summer, fall and winter in Massachusetts, USA. Relative probability of selection is the predicted probability of use for each cover type as a function of temperature. Note, ambient temperature scales differ among seasons and photo-period.

during the day (Fig. 4; Appendix D). K-fold cross validation indicated acceptable model performance across seasons with a mean CCC of 0.75 (0.73–0.88).

Discussion

Moose are extremely well adapted to cold environments, therefore temperatures above their upper critical threshold (UCT) can cause negative direct and indirect effects, which may ultimately lead to declines in populations and local extirpations (Lenarz et al., 2009; Monteith et al., 2015; Murray et al., 2006). In our study area, mean daily temperatures exceeded the lower UCT thresholds of −5 and 14 °C on nearly 90% of the days of the year. By comparison, at the southern boundary of moose range in Minnesota, McGraw et al. (2012) found mean ambient air temperatures to exceed the lower UCT on 50% of the days of the year. We also observed minimum daily temperatures often exceeded the lower UCTs, and on these days ambient temperatures were never within the thermal neutral zone of moose. Conditions outside the thermal neutral zone lasted for extended periods and sometimes for weeks at a time, particularly during summer. However, we also observed moose altering their behavior to utilize land cover types that acted as thermal shelters at temperatures above their UCTs. This behavioral flexibility and the availability of microclimates may explain the ability of moose to expand into and persist in more southern portions of their range.

Vegetation cover can have a large modifying effect on the thermal environment. Closed canopy forests have reduced exposure to solar radiation and cooler temperatures, 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 the ambient air temperature due to the reduction in solar radiation. We detected maximum temperature differences between ambient air temperature and closed canopy coniferous stands of nearly 6 °C in summer. We also observed an increase in temperature differences with increasing temperature, indicating the augmented value of vegetative cover as thermal shelters as temperatures rise, and echoing findings of other studies (e.g., McGraw et al., 2012). Forested wetlands provide the cover benefits associated with closed canopy forests, as well as a medium for conductive cooling with water. Renecker and Hundson (1990) observed that moose decreased respiration from 26 breaths/min when bedded in the shade to 7.5 breaths/min when bedded in a shallow wetland. They also documented a marked decrease in energy expenditure. Demarchi and Bunnell (1993) 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. The use of wetlands can help to accelerate 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 more quickly reduce body temperature.

We observed moose utilizing these cooler cover types when temperatures were high, indicating a thermoregulatory behavioral response. Moose used more open regenerating forest that optimized foraging efficiency when conditions were favorable (e.g., at low temperatures and at night). Conversely, moose greatly reduced use of open foraging habitat and increased their use of forested wetlands and closed canopy forests as temperatures increased. 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 (Demarchi and Bunnell, 1993; Schwab and Pitt, 1991), 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 southerly location of Massachusetts and the thermal conditions relative to other locations where these interactions have been studied.

Our results indicated moose transitioned from selection for regenerating forest to thermal shelters around 16 °C in summer, suggesting heat stress occurred in wild moose at the temperatures identified in captive moose by Renecker and Hudson (1986) and McCann et al. (2013). Additionally, the temperature at which moose transitioned from regenerating forest to thermal shelters in spring and fall (12 °C and 8 °C respectively) supports the hypothesis that moose are most susceptible to thermal stress during these seasons, when they are either shedding or developing their winter coat and when temperatures are high. Moose did alter their habitat selection patterns with increasing temperature in winter, where the transition temperatures were at or just above the 0 °C UCT that triggers thermal panting. 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 Schwab and Pitt, 1991). This indicates, unlike most other areas, moose in Massachusetts are experiencing thermally stressful conditions year round, and not just in the warmer months.

The temperatures we observed in Massachusetts were higher and occurred for longer periods of time compared with temperatures observed in Minnesota moose populations (McGraw et al., 2012). Moose in Massachusetts also showed a stronger behavioral response to temperatures as compared with other studies. These results suggest moose are experiencing extreme heat stress. However, unlike the Minnesota populations (Lenarz et al., 2009) and the populations in Utah, Colorado, and Wyoming (Monteith et al., 2015), the moose population in Massachusetts does not appear to be in decline (Wattles and DeStefano, 2011). One possible explanation for this difference is the effectiveness of thermal shelters. Unlike the boreal forests typical of the rest of moose range, moose in Massachusetts occupy a mostly temperate forest zone (Wattles and DeStefano, 2013). The difference in vegetation types may translate into differences in the effectiveness of these cover types to act as thermal shelters; however, further research examining this hypothesis is needed. Another explanation for this difference may be that moose in Massachusetts are not hunted and do not have natural predators. In the absence of natural predators, weaknesses induced by heat stress will not result in higher susceptibility to predation and removes this cause of mortality from the population. Furthermore, Mech and Fieberg (2014) called the results of Lenarz et al. (2009) – that moose population declines were caused by high temperatures – into question. They argued that the declines in the Minnesota moose population coincided with an increase in the wolf population and that predation was the likely cause of increased mortality, not heat stress. The findings of Monteith et al. (2015) could also be a result of an increasing wolf population during the time of their study, and not a result of heat stress.

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 heat stress. Likely some use of open habitats when temperatures were above the UCTs occurred under cloudy, windy, or rainy conditions, which lowered an individual'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.

We had an 85% fix success rate, which is nearing the 80% rate Frair et al. (2004) found to bias regression coefficients using GPS collar data at a 1 h sampling interval. During informal stationary collar tests, we also found that GPS collars in the coniferous forest cover type had a slightly lower fix success rate. Lastly, the resolution of the imagery we used to classify each moose GPS point was slightly finer than the mean GPS location error of the collars. These data inconsistencies may have resulted in slight biases in our results, particularly the underrepresentation of conifer forest. However, the regression coefficients for conifer forest were significant in the models, as were the interaction terms with temperature, indicating strong support for use of this cover type as a thermal shelter for moose.

Moose in Massachusetts displayed a behavioral response to high temperatures by utilizing cooler microclimates. However, we were unable to quantify whether this behavioral response had negative effects on survival, recruitment, and population productivity. Identifying the thresholds at which thermoregulatory behavior in moose results in significant negative fitness consequences would inform our understanding of moose survival at the southern boundary of their range, which is especially important in a rapidly changing climate. The northeast region, which includes Massachusetts, is the fastest warming region of the contiguous United States (Karmalkar and Bradley, 2017). Regional climate models predict that seasonal temperatures in southern New England will increase by 3.1–3.2 °C, 2.1–2.2 °C, 2.5–2.7 °C, and 2.5–2.6 °C in winter, spring, summer, and fall, respectively, by 2070 (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. Climatic warming will occur in concert with other changes such as loss of hemlock due to the widespread occurrence of the hemlock woolly adelgid (*Adelges tsugae*; Orwig et al., 2002), forest loss from development (Foster et al. 2017), and an increase in parasites such as the winter tick (*Dermacentor albipictus*; Rodenhouse et al., 2009; Samuel, 2007). Whether moose will continue to be successful in Massachusetts given a changing landscape and a warming climate remains to be seen.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.mambio.2018.05.009.

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