Lack of behavioral responses of moose (Alces alces) to high ambient temperatures near the southern periphery of their range

Stacey J. Lowe, Brent R. Patterson, and James A. Schaefer

Abstract: Although fundamental factors limiting geographic ranges are understood for many animal species, there is less certainty regarding how such factors influence the behavior of individuals near distributional edges. We tested the hypothesis that climate limits the southern distribution of moose (Alces alces (L., 1758)) by documenting space use and behavior of 36 females at the margin of the species’ range in Ontario, Canada. We assessed temperature differences among habitats and related changes in seasonal habitat use and daily movement patterns in response to temperature. Ambient temperatures frequently exceeded the thresholds of –5 °C (winter) and 14 °C (summer), above which moose are supposed to be thermally stressed. We detected no differences in habitat use relative to thermoregulation thresholds. However, moose exhibited reduced movement when snow was deep and were more active at dawn and dusk. Low variability in temperature among habitat types implied that functional thermal shelters were absent. We suggest that moose in their southern range either ameliorate heat stress at a finer resolution than we measured or are more resilient to temperature than previously thought. Additional evidence linking temperatures with negative responses is necessary before the prevalent hypothesis of heat stress limiting the southern distribution of moose can be fully assessed.

Résumé : Alors que les facteurs fondamentaux qui limitent les aires géographiques sont bien connus pour plusieurs espèces animales, il est moins clair comment ces facteurs influencent les individus habitant près des marges de ces aires de répartition. Nous testons l’hypothèse qui veut que les conditions climatiques limitent la répartition vers le sud de l’original (Alces alces (L., 1758)) en étudiant l’utilisation de l’espace et le comportement de 36 femelles à la limite de l’aire de répartition de l’espèce en Ontario, Canada. Nous avons mesuré les différences de température entre les habitats et noté les changements associés dans l’utilisation saisonnière des habitats et les patrons de déplacements journaliers en réaction à la température. Les températures dépassaient souvent les seuils de –5 °C (hiver) et 14 °C (été), en-deçà et au-delà desquels les orignaux sont sensés subir un stress thermique. Nous ne décelons aucune différence dans l’utilisation de l’habitat en fonction des seuils de thermorégulation. Cependant, les orignaux se déplacent moins quand la neige est profonde et ils sont plus actifs à l’aube et à la tombée du jour. La faible variabilité entre les types d’habitats fait qu’il n’existe pas de refuges thermiques fonctionnels. Nous croyons que les orignaux dans le sud de leur aire de répartition ou bien mitigent leur stress thermique à une échelle plus fine que celle que nous utilisons ou alors sont plus résistants à la température qu’on ne le croyait antérieurement. Il faudra des données supplémentaires reliant les températures à des réactions négatives avant que l’hypothèse actuelle selon laquelle le stress dû à la chaleur limite la répartition des orignaux vers le sud puisse être complètement évaluée.

Introduction

The study of factors and processes driving limits in the geographic range of species has provided many insights regarding ecological and evolutionary adaptations of animals (e.g., Gaylord and Gaines 2000; Holt and Keitt 2000; Clarke 2003). Although research has addressed the intrinsic and extrinsic determinants of species’ distributional limits (Gaston 2003; Lomolino and Heaney 2004; Canadell et al. 2007), there remain fundamental, unanswered questions regarding how and why geographic ranges of many species appear as they do. This is not surprising given that species’ ranges frequently result from many complex factors acting in a dynamic manner (Gaston 2003). Increasingly, climate is seen as playing a fundamental role in determining range limits, although the specific mechanisms by which such influences are manifested can vary widely (e.g., Parmesan et al. 2000; McCarty 2001; Gaston 2003). In response to climate change, pole-ward shifts in species distributions have been predicted (Walther et al. 2002; Humphries et al. 2004; Intergovern-
mental Panel on Climate Change 2007) and demonstrated (Parmesan and Yohe 2003). It follows that understanding how species respond to temperature extremes at their range limits is critical for predicting long-term shifts in their distribution and abundance.

As warming trends alter ambient temperatures and natural vegetation communities, animal populations occurring at distributional edges may be increasingly subject to daily and seasonal weather extremes outside their tolerable ranges (Walther et al. 2002). In such cases, animals should exhibit either behavioral or physiological mechanisms that provide relief from heat or cold stress if ambient conditions truly are limiting. In general, behavioral responses may be more prevalent than physiological ones owing to their higher efficacy and lower energetic cost (Maloney et al. 2005). Also, animals may exhibit a range of simultaneous behaviors (e.g., heat avoidance through microhabitat selection or altered activity patterns) to heat or cool their body (Cain et al. 2006). Thus, the processes by which animals respond to ambient temperature extremes can be both complex and difficult to isolate from responses to other limiting factors such as food or predation risk.

Moose (Alces alces (L., 1758)) are presumably well adapted to temperate climates (Telfer 1984), but may be subject to thermoregulatory constraints when ambient temperatures exceed upper critical limits (Dussault et al. 2004). To date, only one study has established critical temperature thresholds inducing heat stress in moose through the estimation of heart, metabolic, and respiratory rate changes on captive-reared animals in Alberta, Canada (Renecker and Hudson 1986). This study estimated moose heat stress thresholds of 14 °C in summer and –5 °C in winter with increased respiration rates, and open mouth panting at 20 °C in summer and 0 °C in winter (Renecker and Hudson 1986). If these reported thresholds and responses are representative of free-ranging animals, moose may be considerably more susceptible than other northern ungulates to heat stress because they have the lowest upper critical temperature and lack extensive capabilities to sweat (Schwartz and Renecker 1998; Dussault et al. 2004). It follows that heat stress may be most pronounced at the southern edge of moose distributions and that over time the southern limit of their range may shift northward as a result of warming temperatures (Murray et al. 2006). Moose in the boreal forest may select thermal shelters (mature conifer stands) in response to high ambient temperature (Dussault et al. 2004), and if moose are resting in the heat rather than moving, this should be reflected in lower movement rates, but it is unclear how overall habitat use patterns of these animals are modified when temperatures rise above critical thresholds.

We used global positioning system (GPS) telemetry to study the habitat use and movement of adult female moose at the southern edge of their distribution in Ontario, Canada, to document behavioral mechanisms indicative of adaptive responses to warm temperatures. Although we did not have a direct measure of moose activity, the correspondence between movement rates and activity has been well established for a number of vertebrates, including coyotes (Canis latrans Say, 1823) (Patterson et al. 1999; Way et al. 2004); gray wolves (Canis lupus L., 1758) (Merrill and Mech 2003; Theuerkauf et al. 2003), and white-tailed deer (Odocoileus virginianus (Zimmermann, 1780)) (Holzenbein and Schwede 1989; Rhoads et al. 2010). Moose will reduce movement in deep snow during the winter to conserve energy (Coady 1974); therefore, we expected that moose would employ behavioral energetic conservation strategies such as bedding down in cooler areas (and therefore moving shorter distances) when subjected to heat stress. We predicted that conifer stands would provide cooler ambient temperatures than more open habitats. Thus, when temperatures exceeded critical thresholds, we expected moose to (i) make greater proportionate use of conifer stands, (ii) move shorter distances, and (iii) move primarily during the night.

Materials and methods

Study area

We studied moose in central Ontario, Canada (45°N, 78°W), within the western region of Algonquin Provincial Park (APP) (1640 km²) and southeastern portion of Wildlife Management Unit (WMU) 49 (1300 km²) (Fig. 1). This study area was near the southern distribution of moose range in Ontario (Forbes and Theberge 1993) and occupied the northern portion of the Great Lakes–St. Lawrence Forest Region near the convergence with the boreal forest (Cook et al. 1999). The two study sites were separated by roughly 50 km, with APP consisting of a protected forest with limited moose harvest and logging and WMU 49 including public and private lands where logging and moose harvest occurred. Forest cover in APP was dominated by sugar maple (Acer saccharum), poplar (Populus spp.), American beech (Fagus grandifolia), yellow birch (Betula alleghaniensis), eastern hemlock (Tsuga canadensis), spruce (genus Picea A. Dietr.), and fir (genus Abies P. Mill.); the forest composition in WMU 49 was comparable, although with lower abundance of hemlock and more developed and agricultural land and habitat fragmentation. The study sites differed in elevation, with APP (320–580 m above sea level) approximately 200 m higher than WMU 49 (73–549 m above sea level). Environmental conditions during our study were typical for the area, with the exception of heavy snowfall in 2005 and warmer than average winter temperatures in 2006 (January mean temperature of –5 °C) and 2008 (January mean temperature of –6 °C). From 1971 to 2004, the long-term normal for daily mean temperatures in January and July averaged –11 and 18 °C, respectively (APP, East Gate Station: 45°31’N, 78°16.2’W; Environment Canada 2008).

Collar deployment and monitoring

During January and February 2006, 39 adult female moose (age = 4 ± 2 years (mean ± SD); range = 1–9 years) were captured via aerial net gunning and fitted with Lotek 3300 (Lotek Wireless Inc., Newmarket, Ontario, Canada) GPS collars (APP: n = 20; WMU 49: n = 19; Bighorn Helicopters Inc., Cranbrook, British Columbia, Canada). In addition, during March 2007, 3 new moose were collared via aerial darting using a mixture of carfentanil (Wildlife Pharmaceuticals Inc., Ft. Collins, Colorado, USA) at approximately 0.0070 mg/kg combined with xylazine hydrochloride at approximately 0.2 mg/kg. This drug combination was reversed with naltrexone at approximately 0.7 mg/kg. GPS
collars \( n = 42 \) were programmed to obtain a location fix every 2 h for approximately 2.5 years. Moose location data were retrieved either by recapture and removal of the collars in late-winter 2008 \( n = 37 \) or from carcasses of moose that died during the study \( n = 5 \). All capture and handling methods were approved by the Trent University Animal Care Committee, as well as the Ontario Ministry of Natural Resources.

**Habitat classification**

The forest resource inventory (FRI) data layer used for assigning habitat classifications for moose locations was validated for accuracy via ground-truthing in summer 2007. We accommodated inaccuracies in map classification (Maxie et al. 2010) by condensing forest-type classes into seven broader categories for analysis: HARDWOOD, CONIFER, MIXED, HEMLOCK, WATER, WETLAND, and OTHER (Table 1; for complete category descriptions see Maxie et al. 2010). Additionally, we partitioned WATER into two classes: <100 m from shoreline as SHALLOW WATER and >100 m from shoreline as DEEP WATER. All forest stand age classes, harvested stands, and recent burns were combined into respective habitat classes based on species composition to maintain a small number of habitat classes and owing to homogeneity within age classes.

**Ambient temperature measurement**

We used temperature data collected from Environment Canada weather stations in each study area to describe temperature conditions throughout our study period. In addition, we determined habitat-specific ambient temperature profiles by deploying temperature data loggers \( n = 140 \); Thermo-chron ibuttons, DS1921G-F5; Dallas Maxim Corporation, Dallas, Texas, USA) in 70 stands of the four dominant forest classes (CONIFER, HARDWOOD, MIXED, and HEMLOCK) and in one nonforest habitat type (WETLAND). Forested stands and WETLAND areas located within <1 km of primary and secondary roads in APP were selected randomly and data loggers were affixed to the north side of a tree >50 m from the edge of the stand and 1.5 m from ground level; in WETLAND areas, data loggers were attached to trees, snags, or alder \( (Alnus\ spp.) \) branches. Two data loggers were deployed at each location, which allowed for continuous time measurement of temperature at 2 h intervals for 1 year. All sites were assessed for classification accuracy using prism sweeps along transects. For detailed methods of stand selection and accuracy assessment see Maxie et al. (2010).

**Data analysis**

We analyzed habitat use for each moose by combining GPS collar location data and the FRI digital map in ArcMap and ArcGIS version 9.0 (Environmental Systems Research Institute, Inc. 2004). First, we censored GPS location data on the day of initial capture and recapture, when no location fix was obtained owing to unavailable satellites or other GPS error, or if a location occurred >5 km from the edge of all other used areas (i.e., spatial outliers likely owing to GPS location error rather than a true excursion by the animal). Based on biological knowledge of the local moose population, we established two seasons reflecting periods of susceptibility to heat stress and when temperature thresholds (Renecker and Hudson 1986) and corresponding moose behavioral responses should be consistent (summer: 16 June – 15 September; winter: 1 November – 30 April). Preliminary analysis indicated that differences in index of habitat use between APP and WMU 49 were small and largely owing to differences in availability rather than moose behavior, and therefore we combined moose from both study areas for all further analyses (Lowe 2009).

We calculated utilization distributions (UDs) to determine intensity of use (based on volume under the UD) in each habitat type (Marzluff et al. 2004). UDs were calculated for the 100% isopleths for each moose (within each season) using a fixed kernel density estimator (Marzluff et al. 2004) at a 30 m \( \times 30 \) m raster pixel resolution in Home Range Tools version 1.1 (Rodgers et al. 2007). Kernel bandwidths were estimated using the plug-in bandwidth selection method (Wand and Jones 1995), available in KernSmooth version 2.22 (Ripley 1997) in program R version 2.7.1 (R Development Core Team 2008). We overlaid UD raster layers on the FRI map and calculated volumes in each habitat type to determine probability of use.

We analyzed moose habitat use patterns relative to seasonal upper thermoregulation thresholds and panting thresholds in summer (14 and 20 °C, respectively) and winter (–5 and 0 °C, respectively) (Renecker and Hudson 1986) to assess the influence of ambient temperature on the probability that moose would use a particular habitat type. We collected hourly ambient temperature data spanning the duration of...
the study from public weather stations (APP, East Gate Station: 45°31’N, 78°16.2’W; WMU 49, Beatrice Climate Station: 45°8’N, 79°24.0’W; Fig. 1) (Environment Canada 2008) and related corresponding temperatures in respective study areas with the GPS location data for the same time period for each moose. Within each season, moose locations were partitioned above and below the upper critical limits (UCLs) of the thermoregulatory thresholds (summer: 14 °C; winter: –5 °C) (Renecker and Hudson 1986) according to the temperature at the time the location was recorded. Moose UDs were then calculated for each season so that each UD corresponded to utilization occurring above and below the UCL for each season. Thus, we obtained four UDs for each moose: summer above UCL, summer below UCL, winter above UCL, and winter below UCL. We further tested critical thresholds for moose using temperature thresholds above which moose were reported to exhibit panting behavior (summer: 20 °C; winter: 0 °C) (Renecker and Hudson 1986), and accordingly developed four additional UDs for each moose: summer above 20 °C, summer below 20 °C, winter above 0 °C, and winter below 0 °C.

Within each season, we tested for effects of temperature (above and below the critical thresholds) on probability of use for each habitat type using multivariate analysis of variance (MANOVA) while blocking for individual moose. To increase statistical power, we reduced the number of dependent variables (Stevens 2002) by combining habitat categories that should provide similar thermal cover for moose. We pooled HEMLOCK stands into mixed stands, as HEMLOCK stands in the FRI were composed of as little as 40% hemlock and a mixture of hardwood and conifer species, and presumably contained similar proportions of food and cover as perceived by moose in the mixed stands. We also pooled SHALLOW WATER, DEEP WATER, and WETLANDS into WATER because of the lack of substantial forest cover and because we did not measure ambient temperature differences in either of the open water categories. To attain approximate normal distributions of the response variables, UD proportions were arcsine- and square-root-transformed prior to analysis. We used Wilks’ λ criterion to test for overall significance (Quinn and Keough 2002). Analyses were performed using program R version 2.7.1 (R Development Core Team 2008).

We assessed temperature differences among habitat classes to identify habitat types providing the coolest thermal cover and to determine if this process was dynamic throughout the diurnal cycle. We categorized temperature data recorded from data loggers into habitat classes based on results of the FRE stand validation and to reflect habitat combinations in the thermoregulatory habitat use analysis (CONIFER: n = 7; HARWOOD: n = 26; MIXED: n = 26; WETLAND: n = 11). We used temperature data collected from data loggers from August 2007 (summer) and November and December 2007 (winter) and averaged temperatures within each forest stand for each of six 4 h intervals (0000–0300, 0400–0700, 0800–1100, 1200–1500, 1600–1900, 2000–2300). We used one-way MANOVA to test for effects of habitat type on temperature throughout the day in each season. Post hoc analysis included univariate tests with Bonferroni correction and pairwise comparisons using Tukey’s honestly significant difference (HSD) test. All analyses were performed using program R version 2.7.1 (R Development Core Team 2008).

We examined the daily movement patterns of moose in summer and winter to assess if temperature influenced the timing and distance of movements. We estimated the straight-line distance travelled by each moose between 2 h GPS locations (Hawth’s Analysis Tools version 3.27; Beyer 2004). Each distance was assigned a temperature from the Environment Canada weather station in the respective study area corresponding with the time of the first location in the pair used to calculate the distance travelled for each time interval. Movement distances were log-transformed to improve normality. We calculated a linear regression for every moose within each 2 h time interval in summer and winter. Then we used a Student’s t test with Bonferroni correction to test if the mean of the regression coefficients among moose was different than 0, indicating a response in movement to temperature by moose.

Secondly, we examined the influence of temporal patterns (i.e., frequency and severity) of temperature on within-day

<table>
<thead>
<tr>
<th>Habitat class</th>
<th>APP (%)</th>
<th>WMU 49 (%)</th>
<th>Dominant tree species</th>
</tr>
</thead>
<tbody>
<tr>
<td>HARDWOOD</td>
<td>51</td>
<td>41</td>
<td>Sugar maple (<em>Acer saccharum</em> Marsh.), American beech (<em>Fagus grandifolia</em> Ehrh.), yellow birch (<em>Betula alleghaniensis</em> Britt.), red maple (<em>Acer rubrum</em> L.), northern red oak (<em>Quercus rubra</em> L.), poplar (genus <em>Populus</em> L.), paper birch (<em>Betula papyrifera</em> Marsh.)</td>
</tr>
<tr>
<td>MIXED</td>
<td>12</td>
<td>14</td>
<td>Poplar, red maple, paper birch, balsam fir (<em>Abies balsamea</em> (L.) P. Mill.), sugar maple, eastern white cedar (<em>Thuja occidentalis</em> L.), jack pine (<em>Pinus banksiana</em> Lamb.), black ash (<em>Fraxinus nigra</em> Marsh.)</td>
</tr>
<tr>
<td>HEMLOCK</td>
<td>7</td>
<td>1</td>
<td>Eastern hemlock (<em>Tsuga canadensis</em> (L.) Carr.), yellow birch, sugar maple</td>
</tr>
<tr>
<td>WETLAND</td>
<td>8</td>
<td>9</td>
<td>Brush and alder (genus <em>Alnus</em> P. Mill.), open muskeg, treed muskeg</td>
</tr>
<tr>
<td>DEEP WATER</td>
<td>4</td>
<td>3</td>
<td>Water &gt;100 m from shoreline</td>
</tr>
<tr>
<td>SHALLOW WATER</td>
<td>8</td>
<td>5</td>
<td>Water &lt;100 m from shoreline</td>
</tr>
<tr>
<td>OTHER</td>
<td>1</td>
<td>14</td>
<td>Roads, developed or agricultural land, exposed rock (sparsely vegetated), unclassified habitat</td>
</tr>
</tbody>
</table>

Table 1. Dominant tree species and proportional availability within combined habitat classes in the forest resource inventory (FRI) data layer for the Algonquin Provincial Park (APP) and Wildlife Management Unit (WMU) 49 study areas, central Ontario, Canada.
movement patterns of moose. We generated a heat index (HI) from the hourly temperature data where we calculated the magnitude (°C) that the temperature exceeded the upper critical thresholds in summer (14 °C) and winter (−5 °C) and multiplied it by the duration (consecutive number of hours) that the temperature remained above the respective thresholds (i.e., HI 20 = (magnitude at 10 °C) × (duration of 2 h)). The resulting HI values were divided into three percentile groups in the summer: <1 degree-hours (low), 1–77 degree-hours (moderate), and 78–1010 degree-hours (severe). The response variables (the distance travelled within each time interval) were log-transformed to improve normality and individual moose were treated as a blocking factor. We used MANOVA to analyze the effects of the HI groups on within-day patterns of movement by moose.

The resulting HI values in the winter were <1 degree-hours (low), 2–148 degree-hours (moderate), and 149–6039 degree-hours (severe). To control for the effects of snow on moose movements, we collected the daily maximum snow depth at the Environment Canada weather stations (Fig. 1) for each corresponding day of winter. We divided winter days into three percentile groups and snow index (SI) categories (<6 cm (low), 7–42 cm (moderate), and 43–87 cm (high)) and assigned the corresponding SI category for each day to every movement distance that occurred within that day. We used a two-way MANOVA to analyze the effect of snow depth and heat stress on movement patterns of moose during the winter following the same procedure as the analysis of the summer data.

**Results**

**Temperature conditions**

Ambient temperature was >14 °C for 65% (2870 readings) of the summer readings; on average, it exceeded 14 °C for a considerable portion of the day (16 ± 6 h (mean ± SD), n = 2870 readings). The mean magnitude of temperature exceeding 14 °C was 6 ± 4 °C (n = 2870 readings). The greatest deviation above a temperature threshold that we recorded was 19 °C in the first week of August 2006. The longest duration (consecutive number of hours) that temperatures remained above this threshold occurred in late July 2006 for 137 h (~5.7 days). Ambient temperature exceeded the panting threshold (20 °C) less frequently (30.9%, n = 1365 readings) and was above the threshold for a shorter fraction of the day (7 ± 6 h (mean ± SD), n = 1365 readings). Similarly, moose critical temperature thresholds were commonly exceeded in winter, with temperatures greater than −5 °C occurring 54.9% (5392 h) of the study period and, on average, temperature was above the threshold for roughly half of the day (13 ± 10 h (mean ± SD), n = 5392 readings). The mean magnitude of temperature exceeding −5 °C was 6 ± 5 °C (mean ± SD), n = 5392 readings). The greatest deviation above a temperature threshold that we recorded was 29 °C in late April 2007. The longest duration that temperatures remained continuously above the threshold in winter occurred in late April 2007 for 472 h (~19.5 days). Likewise, the winter panting threshold (0 °C) was exceeded for 29.6% (n = 2902 h) of the study period and, on average, temperatures were >0 °C for the majority of daylight hours (7 ± 9 h (mean ± SD), n = 2902 readings) (Environment Canada 2008).

**Thermal cover**

During the summer, all habitat classes greatly exceeded the 14 °C threshold for a large extent of the day (and partially during the night), except from approximately 0000–0700 when WETLAND and CONIFER dropped approximately 3 °C below the threshold. Likewise, in winter, the mean temperature was above the −5 °C threshold in all habitat types almost continuously during daylight hours (from ~0800 to 1600). The four cover types differed in their ambient temperature profiles during both summer (Wilks’ λ = 0.152, F18,173 = 9.1, P < 0.001; Fig. 2) and winter (Wilks’ λ = 0.283, F18,173 = 5.4, P < 0.001). All habitats exhibited high diurnal variation, but qualitatively the differences between habitat types were relatively modest (Figs. 2, 3). The sole exception was WETLAND, where summer temperature rose rapidly from early morning to the mid-afternoon peak (Δ = −10 °C). Although temperatures during the summer differed among habitat types in each time interval (all P < 0.001), WETLAND emerged as the primary habitat class contributing to observed differences in pairwise comparisons. WETLAND was warmer than all habitat types at most times during the day and cooler at night (Tukey’s HSD, all P < 0.005; Table 2). During winter the temperature profile was
Table 2. Differences in mean temperatures among habitat types in summer (August 2007) and winter (November and December 2007) within the six time intervals.

<table>
<thead>
<tr>
<th>Habitat class</th>
<th>0000–0300</th>
<th>0400–0700</th>
<th>0800–1100</th>
<th>1200–1500</th>
<th>1600–1900</th>
<th>2000–2300</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Summer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HARDWOOD–CONIFER</td>
<td>1*</td>
<td>2*</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>MIXED–CONIFER</td>
<td>1*</td>
<td>1*</td>
<td>3*</td>
<td>3*</td>
<td>1</td>
<td>2*</td>
</tr>
<tr>
<td>WETLAND–CONIFER</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>MIXED–HARDWOOD</td>
<td>3*</td>
<td>3*</td>
<td>3*</td>
<td>3*</td>
<td>2*</td>
<td>2*</td>
</tr>
<tr>
<td>WETLAND–HARDWOOD</td>
<td>2*</td>
<td>2*</td>
<td>3*</td>
<td>3*</td>
<td>1*</td>
<td>2*</td>
</tr>
<tr>
<td>WETLAND–MIXED</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Winter</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>HARDWOOD–CONIFER</td>
<td>0</td>
<td>0</td>
<td>ns</td>
<td>1</td>
<td>ns</td>
<td>0</td>
</tr>
<tr>
<td>MIXED–CONIFER</td>
<td>0</td>
<td>0</td>
<td>ns</td>
<td>0</td>
<td>ns</td>
<td>0</td>
</tr>
<tr>
<td>WETLAND–CONIFER</td>
<td>1*</td>
<td>1*</td>
<td>ns</td>
<td>2*</td>
<td>ns</td>
<td>1*</td>
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<tr>
<td>MIXED–HARDWOOD</td>
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<td>0</td>
<td>ns</td>
<td>0</td>
<td>ns</td>
<td>0</td>
</tr>
<tr>
<td>WETLAND–HARDWOOD</td>
<td>1*</td>
<td>1*</td>
<td>ns</td>
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<td>ns</td>
<td>1*</td>
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<tr>
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<td>ns</td>
<td>1*</td>
<td>ns</td>
<td>1*</td>
</tr>
</tbody>
</table>

Note: Pairwise comparisons (Tukey’s honestly significant difference (HSD) test) within the same column and season ($P < 0.01$). ns indicates nonsignificant ANOVA result, therefore no Tukey’s HSD was performed.

Fig. 4. Probability of summer habitat use by moose (*Alces alces*) ($n = 36$) in central Ontario, Canada (Algonquin Provincial Park (APP) and Wildlife Management Unit (WMU) 49), relative to upper critical temperature limit threshold ($14^\circ$ C) for thermoregulation and panting temperature threshold ($20^\circ$ C) for moose in summer. Probability of use represents mean utilization distribution (UD) for specified temperature category. Error bars represent ±1 SE.

Fig. 5. Probability of winter habitat use by moose (*Alces alces*) ($n = 36$) in central Ontario, Canada (Algonquin Provincial Park (APP) and Wildlife Management Unit (WMU) 49), relative to the reported upper critical temperature limit threshold ($–5^\circ$ C) for thermoregulation and the reported panting temperature threshold ($0^\circ$ C) for moose in winter. Probability of use represents mean utilization distribution (UD) for specified temperature category. Error bars represent ±1 SE.

Thermoregulatory habitat use

We included location data from 36 radio-collared moose in our analysis (APP: $n = 19$; WMU 49: $n = 17$; ~302,000 GPS locations). We censored moose that either died within the first year ($n = 5$) or had collar failures ($n = 1$). Overall, we observed no differences in moose behavior relative to temperature thresholds. Specifically, we found no difference in proportion of habitat types used above versus below the published UCL either in summer (Wilks’ $\lambda = 0.745$, $F[5,31] = 2.1$, $P = 0.09$; Fig. 4) or winter (Wilks’ $\lambda = 0.729$, $F[5,31] = 2.3$, $P = 0.07$; Fig. 5). This finding was counter to the predicted increase in use of CONIFER (thermal cover) and decrease in use of HARDWOOD (feeding areas) at high temperatures. Surprisingly, mean probability of CONIFER use increased only ~2% in summer and 1% in winter when...
temperatures were above the threshold, and mean probability of use of HARDWOOD increased <0.5% in summer but decreased <0.5% in winter. Similarly, we detected no differences in probability of habitat use above versus below the reported panting threshold (summer: Wilks’ $\lambda = 0.751$, $F_{[5,31]} = 2.1$, $P = 0.10$ (Fig. 4); winter: Wilks’ $\lambda = 0.756$, $F_{[5,31]} = 1.9$, $P = 0.11$ (Fig. 5)), with moose use of CONIFER increasing <2% above the panting threshold in summer and winter.

Within-day movement patterns

The linear relationship between temperature and distance of movement was significant, and positive, for the majority of the time intervals in both seasons, but the mean increase in movement as temperature increased was only <1% (Student’s $t$ test, $P < 0.05$; summer range ~1.0% to 1.9%; winter range ~0.4% to 1.1%) in both seasons. The mean difference in movement among the three levels of heat stress in summer (low, moderate, and severe) was significant (MANOVA: Wilks’ $\lambda = 0.180$, $F_{[2,35]} = 6.7$, $P < 0.01$), but qualitatively the differences were relatively small throughout the day (Fig. 6), indicating that partitioning the data by temperature severity (magnitude and duration of high temperatures) failed to adequately explain variation in movement by moose during the summer. The effect of heat stress and snow depth on moose movement distances in winter was also statistically significant (Figs. 7a–7c; Wilks’ $\lambda = 0.416$, $F_{[4,35]} = 5.5$, $P < 0.01$), but again, qualitatively differences were small and not indicative of biologically meaningful behavioral responses by moose to ameliorate heat stress. However, moose exhibited a strong decrease in movement with increasing snow depth (Fig. 8). Overall, we conclude that behavioral responses by moose to heat stress were minimal in both summer and winter. Moose movements, however, were influenced by other factors including (i) time of day, as moose exhibited a crepuscular activity pattern in both

**Fig. 6.** Mean distance of movement by GPS-collared moose (*Alces alces*) ($n = 36$) in 2 h time intervals during summer in relation to heat index (HI) levels (low HI: <1 degree-hours; moderate HI: 1–77 degree-hours; severe HI: 78–1010 degree-hours) in central Ontario, Canada.

**Fig. 7.** Mean distance of movement by GPS-collared moose (*Alces alces*) ($n = 36$) in 2 h time intervals throughout the day in winter at varying snow depths ((a) high: 43–87 cm; (b) moderate: 7–42 cm; (c) low: <6 cm) and at varying heat index (HI) levels (low HI: <1 degree-hours; moderate HI: 2–148 degree-hours; severe HI: 149–6039 degree-hours) in central Ontario, Canada.
seasons (Figs. 6, 7a–7c), and (ii) reduced daily movement in response to high snow depths in the winter (Fig. 8).

Discussion

From a behavioral perspective, individuals respond to daily and seasonal pressures by making frequent trade-offs to maintain a positive energy budget or to reduce the energy deficit (Schwartz and Renecker 1998). Dussault et al. (2005) suggested that moose habitat selection is a hierarchical process where patterns reflect the importance of limiting factors for individual fitness. If temperature is an important factor governing fitness, then we expect habitat use and movement patterns to be influenced by temperature, especially when it exceeds upper critical limits and induces heat stress. Furthermore, we expect that if temperature is the most critical limiting factor for moose, then responses should be obvious and evident at a coarse scale of habitat use.

Evidence for behavioral responses to summer thermal conditions is generally consistent across moose range in North America. Moose in the boreal forest in Quebec used thermal shelters (mature conifer stands) more frequently and were more active at night in summer and fall when temperatures were warm (Dussault et al. 2004). Similarly, Schwab and Pitt (1991) found that moose in British Columbia selected mature forest to relieve heat stress when operative temperatures exceeded critical limits. Additionally, moose in Alberta reduced both energy expenditure and respiratory rates by bedding in wet meadows in the summer (Renecker and Hudson 1990).

Our results did not fully concur with these findings, as we failed to detect a clear relationship between habitat use and high temperatures in our study area in summer (Fig. 4) or winter (Fig. 5) at the thresholds that we tested. However, we could not determine the degree to which crepuscular movements may reflect attempts to ameliorate heat stress. Interestingly, only Schwab and Pitt (1991) reported evidence of habitat selection behavior to relieve heat stress in winter, yet our early winter temperature profiles indicate, on average, all habitat types surpassed the threshold ~33% of the day.

Overall, moose habitat utilization closely corresponded to proportional availability of habitat classes in each study area (Table 1). This was not altogether surprising given that (i) moose are typically habitat generalists (Belovsky 1981); (ii) food and predation did not appear to be limiting during the study (i.e., physical condition appeared good and survival was high; D.L. Murray, unpublished data); and (iii) all of the habitat types were highly interspersed within the landscape, thereby likely providing access to each forest type within each home range (S.J. Lowe, unpublished data).

Variation in ambient temperatures among forested habitat types in our study area was minimal at the spatial and temporal resolutions that we tested. Differences in temperature were most likely to occur between open and closed canopies during the day, and differences among habitat types were more pronounced in summer (Figs. 2, 3). Therefore, at the macrohabitat (forest stand) scale, our study area appears devoid of strong thermal gradients for moose. Lack of differences may be attributed to the composition of the study areas being mostly similar-aged stands where sufficient shade is available in all habitat types.

We also failed to detect consistent differences in distances of movement by moose in response to temperature (Figs. 6, 7a–7c). If moose employed behavioral adaptations to cope with unfavorable temperatures, then we should have observed decreased daily movement during periods of heat stress and increased nocturnal behavior when temperatures became extreme during the day. Yet, the relationship between temperature and movement was weak throughout the day in both seasons. Even when we considered the effects of the duration and magnitude of temperature above the threshold for moose, we failed to detect an obvious behavioral response. Moose movement (and therefore habitat use behavior) may be suppressed owing to increased energy demands of locomotion in deep snow (Renecker and Schwartz 1998). Throughout our study, snow depths rarely exceeded the lowest snow depth threshold reported to impede movement by moose (50 cm; Geist 1998) with the exception of 2006 (>50 cm for 42.5% (51 days) in 2006, 6% (0 days) in 2007, and 5.4% (9 days) in 2008), during which moose were monitored only after mid-January (Lowe 2009). However, we detected a strong negative correlation in mean daily movement distances with increasing snow depth (Fig. 8). We interpret this to mean that our data were likely adequate to detect a response to temperature if it had occurred during our study.

Previously reported temperature thresholds for moose may be inaccurate owing to small sample size and the inability to mimic natural conditions using captive individuals in a paddock (n = 2 female moose; Renecker and Hudson 1986). Accordingly, and based on the results of this study, we suspect that the actual upper critical limit of heat stress for moose in both seasons is higher than reported. Quantification of heat stress thresholds may be improved by experimentally testing temperature patterns that could potentially influence the extent of the severity of heat stress in moose. For example, moose are large-bodied mammals that are likely to have high thermal inertia (Renecker and Hudson 1990). Therefore, it may take several consecutive hours to induce heat stress.

Is heat stress a vital limiting factor for moose populations along the southern periphery of their range? Intuitively, we would expect that a large northern ungulate with low toler-
ance for high temperatures would gradually be pushed out of the southern reaches of its range as the climate continues to warm and temperature conditions become increasingly unfavorable. The logic is that persistent temperatures above the upper critical limit will suppress foraging time and consequently cause mass loss during the summer, and that this reduced condition could affect overwinter survival and productivity (Schwartz and Rennieker 1998). If habitat conditions were poor, and if other factors were concurrently limiting (i.e., predation, parasitism), then we would expect individual fitness to decrease and eventually population decline to follow, such as demonstrated for moose in northwestern Minnesota (Murray et al. 2006). We discount the role of heat stress in limiting moose distribution in our region; however, we caution that this phenomenon is still largely untested using empirical data from across the southern distribution of moose range. Also, consideration of alternative scales of habitat use (i.e., bed sites) is warranted in future research. Finally, we recommend a rigorous assessment of critical temperature thresholds on free-ranging moose (including males) to further our understanding of physiological tolerance limits of heat stress in this species.

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