Behavioral responses of moose (*Alces alces*) to ambient temperature: is there evidence for behavioral thermoregulation?

A thesis submitted to the committee of Graduate Studies
in partial fulfillment of the requirements for the degree
of Master of Science in the Faculty of Arts and Sciences

TRENT UNIVERSITY
Peterborough, Ontario, Canada

© Stacey J. Lowe 2009

Environmental and Life Sciences Graduate Program M.Sc.

September 2009
Abstract

Behavioral responses of moose (*Alces alces*) to ambient temperature: is there evidence for behavioral thermoregulation?

Stacey J. Lowe

The understanding of factors and processes driving limitation in the geographic range of species has important implications for conservation and management. I assessed climate as a factor driving moose (*Alces alces*) population limitation near the southern range periphery in Ontario, Canada. I analyzed moose behavioral responses to ambient temperature by comparing habitat utilization profiles above vs. below upper critical temperature thresholds. I also assessed the utility of several habitat types to provide thermal cover for moose. Moose did not alter habitat use patterns relative to high temperatures in summer or winter, and temperatures did not vary substantially among habitats. I interpret these findings as suggestive that moose in central Ontario may be more resilient to temperature extremes than previously expected, but more broadly, my research demonstrates how individual behavior is useful for testing hypotheses at larger scales to determine why animal range limits may be influenced by ongoing climate change.

**Keywords:** *Alces alces*, behavioral thermoregulation, habitat selection, heat stress, moose
Acknowledgements

I especially thank my family for supporting and encouraging me throughout my master’s, but mostly for inspiring me throughout my entire life. I am grateful for the sacrifices they have endured to help me succeed.

I am indebted to Josh Holloway, fellow lab mate and friend, for many stimulating discussions about moose, UDIs, and of course wolves, as well as helping me in the field on several occasions. I also thank him for meaningful suggestions on the analysis and an early draft of the manuscript. I especially thank him for lending me his sincere support every day, and for teaching me so many things, I really appreciate it!

Special thanks to my friend Linz Spenceley for donating so much of her time to downloading and collecting data loggers with me. I also thank her for so many great memories in Peterborough, and all of her friendly support and advice throughout many difficult times.

I also wish to thank Karen Hussey, fellow lab mate studying on the moose project for assisting and sharing in the work load with the logistics of the project. I thank Jean Arseneau and Chris Sharp for volunteering their time in the field. Also, I thank Andrew Silver (MNR) for his outstanding logistical support on various aspects of the field work, and for going out of his way on many occasions to ensure things were done properly.

I thank Dr. Brent Patterson and Dr. Dennis Murray (co-supervisors) for their exceptional assistance and guidance on all aspects of the project. I especially thank Dr. Jim Schaefer (committee member) for temperature data loggers, suggestions on the analysis, and helpful input throughout the project.

Lastly, I thank Jon Moryk for many fishing lessons and adventures and Ashley Spenceley for great times and friendly support.
Table of Contents

ACKNOWLEDGEMENTS ........................................................................................................ II
LIST OF TABLES .................................................................................................................... V
LIST OF FIGURES ................................................................................................................ VI
CHAPTER 1
GENERAL INTRODUCTION ................................................................................................. 1
RANGE LIMITATIONS ......................................................................................................... 1
THERMOREGULATION ........................................................................................................ 2
BEHAVIORAL THERMOREGULATION STRATEGIES ....................................................... 3

CHAPTER 2
BEHAVIORAL RESPONSES OF MOOSE (ALCES ALCES) TO AMBIENT TEMPERATURE: IS THERE EVIDENCE FOR BEHAVIORAL THERMOREGULATION? ................................................................. 6
ABSTRACT ......................................................................................................................... 7
INTRODUCTION ............................................................................................................... 8
METHODS ....................................................................................................................... 11
  Study Area ....................................................................................................................... 11
  GPS Collar Deployment and Monitoring .................................................................. 12
  Habitat Classification ............................................................................................... 13
DATA ANALYSIS ............................................................................................................ 14
  Habitat Analysis ........................................................................................................ 14
  Landscape Habitat Use .......................................................................................... 15
  Thermoregulatory Habitat Use ........................................................................ 16
  Thermal Cover ........................................................................................................... 18
RESULTS ........................................................................................................................ 18
  LANDSCAPE HABITAT USE ...................................................................................... 18
  THERMAL COVER .................................................................................................. 20
  THERMOREGULATORY HABITAT USE .................................................................... 21
DISCUSSION .................................................................................................................... 23

CHAPTER 3
GENERAL CONCLUSION .............................................................................................. 41
FUTURE RESEARCH ..................................................................................................... 44
LITERATURE CITED .................................................................................................... 47
List of Tables

Table 2.1. Description of dominant tree species within combined habitat classes in the Forest Resource Inventory (FRI) data layer for the Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU 49) study areas, central Ontario, Canada…………………37

Table 2.2. Moose habitat use and availability in the Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU 49) study areas in winter and summer. The Index of Use corresponds to results of a one-sample t-test between use and availability; where RANDOM: P>0.05; AVOID: P<0.05, with use being less than available; SELECT: P<0.05, with use being greater than available……………………………………………………..38

Table 2.3. Pairwise comparisons (Tukey’s HSD) in temperature among habitat types in summer and winter; differences within time intervals (T1: 0000-0300; T2 = 0400-0700; T3: 0800-1100; T4: 1200-1500; T5: 1600-1900; T6: 2000-2300) represent °C difference in habitat specific temperature averages for each pairwise comparison performed for summer (August 2007) and winter (November and December 2007)……………………………..39
List of Figures

Fig. 2.1. Location of study areas in Algonquin Provincial Park (APP) and Wildlife Management Unit (WMU) 49 in central Ontario, Canada. The 2 study areas are hatched. Environment Canada weather station locations are indicated by a star. ...............40

Fig. 2.2.a. Proportional summer habitat use by moose in Algonquin Provincial Park (APP) \((n = 19)\) and Wildlife Management Unit 49 (WMU 49) \((n = 17)\) in central Ontario, Canada, compared to proportional study area availability. Proportion of habitat use represents mean Utilization Distribution among moose in summer, and proportion of habitat available represents the proportional availability within the study area. Error bars represent \(\pm 1\) SE. ..........................................................41

Fig. 2.2.b. Proportional winter habitat use by moose in Algonquin Provincial Park (APP) \((n = 19)\) and Wildlife Management Unit 49 (WMU 49) \((n = 17)\) in central Ontario, Canada, compared to proportional study area availability. Proportion of habitat use represents mean Utilization Distribution among moose in winter, and proportion of habitat available represents the proportional availability within the study area. Error bars represent \(\pm 1\) SE. ..........................................................42

Fig. 2.3. Summer mean temperatures among habitat classes throughout the day. Time intervals \((T1: 0000-0300; T2 = 0400-0700; T3: 0800-1100; T4: 1200-1500; T5: 1600-1900; T6: 2000-2300)\) represent habitat specific averages for summer (August 2007); error bars represent \(\pm 1\) SE of temperature means. .........................................................43

Fig. 2.4. Winter mean temperatures among habitat classes throughout the day. Time intervals \((T1: 0000-0300; T2 = 0400-0700; T3: 0800-1100; T4: 1200-1500; T5: 1600-1900; T6: 2000-2300)\) represent habitat specific averages for winter (November and December 2007); error bars represent \(\pm 1\) SE of temperature means. .........................................................44

Fig. 2.5. Probability of summer habitat use by moose \((n=36)\) in central Ontario, Canada relative to the reported upper critical temperature limit threshold \((14^\circ C)\) for thermoregulation, and the reported 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 \(\pm 1\) SE. ............................................................................45
Fig. 2.6. Probability of winter habitat use by moose (n=36) in central Ontario, Canada relative to the reported upper critical temperature limit threshold (-5°C) for thermoregulation, and the reported panting temperature threshold (0°C) for moose in winter. Probability of use represents mean Utilization Distribution (UD) for specified temperature category; error bars represent ± 1 SE.
Chapter 1

General Introduction

The geographic distributions of species are often studied using occurrence data to generate maps depicting range extents at multiple scales. The fallacy of range maps is that species occurrence is rarely continuous with an abrupt edge and population density is seldom uniform throughout the distribution (MacDonald 2003). Species ranges are more often the result of several complex, interacting, and dynamic factors (Gaston 2003). The use of occurrence data to study range limits does not reveal the complex biological interactions that facilitate expansion or contraction of a species’ range. Studying the factors that influence range limits of species provides valuable knowledge for conservation of species, especially along range peripheries (Laliberte and Ripple 2004).

Range Limitations

All species are limited in range, but factors that determine where a species exists may be complex and difficult to isolate, especially where several factors may be interacting concurrently to limit distribution (Krebs 2001). Common factors contributing to range limitations include climate, habitat fragmentation, parasites, predation, and other habitat conditions (Krebs 2001, Gaston 2003). Climate is likely the most studied due to widespread concerns regarding global warming and its potential to impact species that are already imperiled (Thomas et al. 2004).

The restriction of ranges by climate is generally attributed in part to physiological and behavioral adaptations of the species that enable them to survive and reproduce under
a range of climatic conditions often defined by their distribution (Krebs 2001, Gaston 2003). Changes in climate may affect species directly if the local weather regime is altered beyond what is physically tolerable for individuals. Alternatively, climate may affect species indirectly if it alters the distribution or abundance of vegetation and habitat on which a species relies (Johnston and Schmitz 1997). Global mean temperatures have been rising over the last century, and warming has been more pronounced in the last 50 years, especially at higher northern latitudes (Meehl et al. 2007). The Intergovernmental Panel on Climate Change (IPPC) projects global mean temperatures to rise approximately 0.2°C per decade in the next 20 years (Meehl et al. 2007). In North America, mean temperature is expected to rise by approximately 2-3°C in eastern regions and ~5°C in northern regions over the next century (Christensen et al. 2007). Recent studies suggest a northerly shift of the distribution of many species in response to climate warming (Humphries et al. 2004, IPCC 2007, Walther et al. 2002), and populations inhabiting distributional edges may be increasingly subject to daily and seasonal weather conditions that exceed tolerable ranges (Parmesan et al. 2000). These populations in particular warrant further investigation to ascertain the proximate and ultimate causes of limits to their geographic distribution and to provide insight to potential distribution or abundance changes in response to climate warming.

**Thermoregulation**

The immediate thermal environment can inflict stress on individuals, which can affect survival or reproduction directly, or less-directly influence their vulnerability to other biotic factors such as predation or disease (Hoffmann and Parsons 1991). Sibly and
Calow (1989) defined stress as “…an environmental condition that, when first applied, impairs Darwinian fitness, including environmental conditions that decrease survivorship and fecundity as well as growth” (as in Hoffmann and Parsons 1991:2). Hoffmann and Parsons (1991) argue that there is a level of resistance to stress in a species most often indicated by the limit of its geographic range. Furthermore, they suggest that the result of physical stress on the individual is an increase in energy spent on maintenance, to the detriment of investments in growth and reproduction.

Thermoregulation occurs when changes in the ambient temperature rise or fall outside of a species’ thermoneutral zone and an individual must use physiological or behavioral mechanisms to heat or cool its body (Cain et al. 2006). The thermoneutral zone consists of an upper and lower critical ambient temperature threshold within which the animal is not required to increase or decrease heat production by adjusting its metabolic or respiratory rate to maintain homeostasis (Moyes and Schulte 2006). When ambient temperatures change sufficiently to require thermoregulation, mammals may employ several tactics to cope with the unfavorable conditions that include physiological (i.e., sweating, panting) and behavioral mechanisms (i.e., microhabitat selection, altered activity patterns; Cain et al. 2006).

**Behavioral Thermoregulation Strategies**

Behavioral thermoregulation mechanisms are complex and diverse among species, and can also be spatially and temporally dynamic. Behavioral responses include selection for microclimates and altered activity patterns and should be preferred over physiological mechanisms to reduce thermoregulation costs since they are often more
energetically efficient (Maloney et al. 2005, Cain et al. 2006). For example, microhabitat characteristics influenced bed site selection for mule deer (*Odocoileus hemionus*) (Germaine et al. 2004) and elk (*Cervus elaphus*) (Millspaugh et al. 1998) due to thermoregulatory advantages. Similarly, desert bighorn sheep (*Ovis canadensis mexicana*) preferred to use microclimates in caves and under the shade of trees where temperatures were cooler and provided more thermal relief from heat stress than open areas (Cain et al. 2008). Alteration of activity patterns by individuals may include being active when temperatures are most conducive to energy conservation, or reducing activity levels altogether. For example, black wildebeest (*Connochaetes gnou*; Maloney et al. 2005) and greater kudus (*Tragelaphus strepsiceros*; Owen-Smith 1998) reduced activity levels in response to high ambient temperatures. In desert ungulates, Cain et al. (2006) noted that a combination of timing of activity, use of microclimates, body orientation to the sun, migration, and timing of reproduction were all used to aid in reduction of heat stress. However, thermal shelters were not found to provide any significant energetic advantages or increased productivity for elk in summer and winter in Oregon (Cook et al. 1998). This may imply that although some species exhibit behavioral thermoregulation strategies, the behavioral responses may have little impact on the overall energy budget, and thus only a modest effect on individual fitness.

The hypothesis that behavioral responses may underlie thermoregulatory strategies is potentially applicable to most species. Furthermore, behavioral constraints on thermoregulation may have severe ramifications on population dynamics if fitness is reduced as a result of behavioral responses. Identifying behavioral mechanisms underlying thermoregulation strategies is essential to understanding the behavioral
ecology and parameters that might influence individual fitness and ultimately population
dynamics of a species. Understanding what thermal environments produce sufficient
stress to elicit behavioral responses, and the critical threshold of stress tolerable before
fitness is compromised may provide valid criteria for predicting species persistence in the
future.
Chapter 2

Behavioral responses of moose (*Alces alces*) to ambient temperature: is there evidence for behavioral thermoregulation?
Abstract

There is considerable interest in the study of factors and processes driving limitations in the geographic range of species (Gaston 2003, Krebs 2001). We tested the hypothesis of climatic influence on moose (*Alces alces*) population limitation in the southern-most part of moose range in Ontario, Canada. We documented moose behavior over 2.5 years via relocation fixes from GPS collars attached to 36 adult female moose in and around Algonquin Provincial Park, and compared habitat utilization profiles above vs. below upper critical temperature thresholds for moose in summer and winter. We also assessed ambient temperature differences among habitat types to assess the optimal thermal shelters for moose throughout the day. Moose did not alter habitat use patterns relative to high ambient temperatures in summer or winter at either of the thresholds we considered. We also found ambient temperatures were strikingly similar among habitat types in our study area, and thus at the macrohabitat scale, our study area was likely devoid of forested thermal shelters for moose. Surprisingly, temperatures during our study exceeded the putative thermoregulation thresholds for moose extensively in summer and winter, yet we failed to detect a difference in proportion of habitat types used by moose above vs. below these thresholds. Contrary to our expectations, this moose population may be more resilient to high temperatures than previously suggested, and we recommend rigorous testing of upper critical temperature limits that induce heat stress in free ranging moose to further our understanding of physiological tolerance limits to temperature.

**Keywords:** *Alces alces*, behavioral thermoregulation, habitat selection, heat stress, moose
**Introduction**

The study of factors and processes driving limits in the geographic range of species has revealed a variety of insights regarding ecological and evolutionary adaptations of animals (e.g., Clarke 2003, Gaylord and Gaines 2000, Holt and Keitt 2000). To date, research has addressed the intrinsic and extrinsic determinants of species’ distributional limits (Canadell et al. 2007, Gaston 2003, Lomolino and Heaney 2004), yet there remain fundamental unanswered questions regarding how and why geographic ranges of many species appear as they do. This should not be surprising given that species ranges are frequently the result of 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 manifest can vary widely (e.g., Gaston 2003, McCarty 2001, Parmesan et al. 2000). In some cases, a poleward shift in species distribution is predicted in response to climate warming (Humphries et al. 2004, Intergovernmental Panel on Climate Change 2007, Walther et al. 2002), and it follows that understanding how species that are sensitive to climate respond to temperature extremes at their range limit is critical for predicting their long-term shifts in distribution and abundance.

Populations occurring at distributional edges may be increasingly subject to daily and seasonal weather extremes outside their tolerable ranges as warming trends alter temperatures (Walther et al. 2002). In such cases, animals should exhibit either behavioral or physiological mechanisms that improve thermoregulation and relief from heat or cold stress, if ambient conditions truly are limiting. In general, behavioral responses may be more prevalent than physiological ones due to their increased efficacy
and reduced energetic cost (Maloney et al. 2005), and there may be a range of behaviors (e.g., heat avoidance through microhabitat selection or altered activity patterns) exhibited by animals that reflect attempts to heat or cool their body (Cain et al. 2006). However, behavioral thermoregulation mechanisms are multifaceted and diverse among species, and may be difficult to relate directly to population level effects due to complex features of the spatial and temporal scales involved and concurrent interactions with other limiting factors.

Moose (Alces alces) are thought to be well adapted to temperate climates (Telfer 1984), but may be subject to thermoregulatory constraints when ambient temperatures exceed upper critical limits for the species. To date, only one study has reported critical temperature thresholds inducing heat stress in moose; upper critical temperature limits were estimated from heart, metabolic, and respiratory rate changes on 2 captive-reared female moose in Alberta, Canada (Renecker and Hudson 1986). Heart rate and metabolic rates were stimulated and indicated heat stress occurs at thresholds of 14°C in summer and -5°C in winter. Furthermore, respiration rates increased and moose exhibited open mouth panting at 20°C and 0°C in summer and winter, respectively (Renecker and Hudson 1986). Accordingly, moose may be the most susceptible of all northern ungulates to heat stress because they have the lowest upper critical temperature and lack extensive sweating capabilities (Schwartz and Renecker 1998, Dussault et al. 2004). It follows that moose may be particularly vulnerable to heat stress near the southern edge of their distribution, and that over time the southern limit of their range may shift northward as a result of climate warming (Murray et al. 2006). Alternatively, moose populations may respond locally to weather extremes through adaptive mechanisms that allow them
to co-exist with inclement weather conditions. Currently, it is uncertain the extent to which southern moose populations respond adaptively to temperature extremes.

Moose in the boreal forest region may select mature conifer stands (thermal shelters) in response to high ambient temperature (Dussault et al. 2004), but it is unclear how the overall habitat-utilization profile of such animals is modified when environmental conditions fall above critical thresholds. Further, the presently accepted critical temperature limits for moose (Renecker and Hudson 1986) may not be relevant to free-ranging moose in all areas of their range so alternative thresholds may need to be identified and assessed. At the very least, given the limited data on which the thresholds identified by Renecker and Hudson (1986) were based, researchers should consider multiple thresholds for moose responses to temperature while exploring changes in overall habitat use patterns.

We utilized GPS telemetry to study adult female moose habitat use at the southern edge of their distribution in Ontario, Canada to document behavioral mechanisms indicative of adaptive responses to a range of hypothesized critical temperature thresholds. We expected to observe substantial changes in habitat use patterns when moose were potentially heat stressed, and predicted that cooler habitats would be preferred. Moreover, we tested the efficacy of forest habitat types to provide thermal cover for moose in winter and summer at the southern edge of the distribution.
Methods

Study Area

We studied moose behavior in central Ontario, Canada (45°N, 78°W) within the western region of Algonquin Provincial Park (APP) (1,643 km²) and Wildlife Management Unit (WMU) 49 (1,299 km²) (Fig. 2.1). 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 approximately 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 included sugar maple (Acer saccharum), poplar (Populus spp.), American beech (Fagus grandifolia), yellow birch (Betula alleghaniensis), eastern hemlock (Tsuga canadensis), and spruce (Picea spp.)/fir (Abies spp.); the forest composition in WMU 49 was comparable, although with lower abundance of hemlock and more developed/agricultural land and habitat fragmentation. The study sites differed in elevation, with APP (320 m-580 m) being approximately 200 m higher than WMU 49 (73 m-549 m). Reported moose density estimates based on aerial survey data were similar: 0.30 moose/km² in APP (2006) and 0.29 moose/km² in WMU 49 (2005) (Ontario Ministry of Natural Resources (OMNR) unpublished data). Predators of moose in both study areas included wolves (Canis spp.) and black bears (Ursus americanus).

Environmental conditions during our study period were typical for the area, with the exception of heavy snowfall in 2006 and warmer than average winter temperatures in
The daily average temperatures for January and July were approximately –11°C and 18°C, respectively. Historical averages for winter (November-April) snow depth in the region were approximately 43 cm, whereas during our study winter average and maximum snow depth varied from 52 cm and 81 cm during 2006 to 15 cm and 39 cm during 2007, respectively (APP East Gate Station: 45° 31.8’N 78° 16.2’W; Environment Canada 2008).

**GPS Collar Deployment and Monitoring**

During January and February of 2006, 39 adult (mean age = 3.8 ± 2.0 (SD) years; range: 1-9 years old) female moose were captured via aerial net gunning and fitted with Lotek 3300 (Lotek Wireless Inc., Newmarket, ON, Canada) Global Positioning System (GPS) collars (APP: \( n = 20 \) moose; WMU 49: \( n = 19 \) moose; Bighorn Helicopters Inc., Cranbrook, BC, 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/ cc combined with xylazine hydrochloride at approximately 0.2 mg/ cc. This drug combination was reversed with naltrexone at approximately 0.7 mg/ cc. GPS collars (\( n = 42 \)) were programmed to obtain a location fix every 2 hours for approximately 2.5 years. Moose location data were retrieved either by recapture and removal of the collars in late winter 2008 (\( n = 37 \) moose) or from carcasses of moose that died during the study (\( n = 5 \)). All 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 relocations was validated for accuracy in summer 2007. We accommodated inaccuracies in map classification (Maxie et al. *in press*) by condensing forest-type classes into 7 broader categories for analysis: HARDWOOD, CONIFER, MIXED, HEMLOCK, WATER, WETLAND, and OTHER (Table 2.1; see Maxie et al. *in press* for complete category descriptions). Additionally, we partitioned WATER into 2 separate classes; we applied a 100 m internal buffer to water bodies and reclassified area <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. Differences in stocking density and canopy closure were considered to be minimal due to the same dominant harvesting regime being applied in both study areas (selective and shelterwood harvesting; Maxie et al. *in press*) and the lack of substantial variability in forest stand age classes within habitat types despite harvesting that occurs.

Temperature Data Logger Deployment

We determined habitat-specific temperature profiles by deploying temperature data loggers (n = 140; Thermochron ibuttons, DS1921G-F5; Dallas Maxim Corporation) in 70 stands of the 4 dominant forest classes (CONIFER, HARDWOOD, MIXED, and HEMLOCK) and in 1 non-forest habitat type (WETLAND). Forest stands receiving data loggers were selected randomly from those located within 1 km of a drivable road, 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. Two data loggers were deployed at each location, which allowed for continuous time measurement of temperature at 2-hour intervals for 1 year. Forest stand classification was assessed within each stand using prism sweeps along transects (see Maxie et al. *in press* for methods of stand selection and accuracy assessment).

**Data Analysis**

**Habitat Analysis**

We analyzed moose habitat use patterns to test for behavioral responses to heat stress relative to published seasonal upper thermoregulation thresholds and reported panting thresholds in summer (14°C and 20°C, respectively) and winter (-5°C and 0°C, respectively; Renecker and Hudson 1986). First, we established 2 seasons reflecting periods of susceptibility to heat stress and when temperature thresholds and corresponding moose behavioral responses should be consistent (summer: June 16-September 15; winter: November 1-April 30). We pooled data among years because preliminary analysis indicated that proportional habitat use did not vary among years (S. J. Lowe, unpublished data).

We analyzed habitat use for each moose by combining GPS collar location data and the FRI digital map in a Geographic Information System (GIS) (Arcmap, ArcGIS v. 9.0; ESRI 2004). We censored GPS relocation data for time intervals on the day of initial capture and recapture, when no location fix was obtained due to unavailable satellites or other GPS error, and if a location occurred greater than 5 km from the edge of all other used areas (i.e., spatial outliers likely due to GPS location fix error rather than a true
excursion by the animal). We calculated Utilization Distributions (UDs) to determine intensity of use (based on volume under the UD) in each habitat type (see Marzluff et al. 2004). The advantages of this approach are that relocations used by each animal serve to develop a probability of a particular habitat type being used, and it correctly treats the animal as the experimental unit (Marzluff et al. 2001). UDs were calculated to the 100% isopleths for each moose (within each season) using a fixed kernel density estimator (Marzluff et al. 2004) at a 30 x 30 m raster pixel resolution in Home Range Tools, v.1.1 (Rodgers et al. 2007). Kernel bandwidths were estimated using the plug-in bandwidth selection method (Wand and Jones 1995) available in the package KernSmooth v. 2.22 (Wand 1997) in program R (v. 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.

**Landscape Habitat Use**

We calculated an index of habitat use by comparing probability of habitat use (mean UDs) relative to proportional availability of each habitat class within the landscape to determine if use was as expected (RANDOM), more than expected (SELECT), or less than expected (AVOID) in each study area. We estimated proportional availability by summing the area of each habitat type and dividing by the total area within a minimum convex polygon (Hawth’s Analysis Tools, v.3.27; Beyer 2004) (see Fig. 2.1) derived from all moose relocations in respective study areas on the FRI layer. UD and proportional availability data were arcsine square-root transformed to attain approximate normal distributions, and were analyzed using a one-sample t-test. We assigned each
habitat an index of use based on significance of the t-test and directionality of difference between mean use and proportional availability. If there was no difference between use and availability ($P>0.05$), the use index was classified as RANDOM. If mean use was less than available ($P<0.05$), use was categorized as AVOID, and if mean use was greater than available ($P<0.05$), use was categorized as SELECT. We qualitatively compared the Index of Use in each season between study areas because we suspected the indices of use (i.e., RANDOM, SELECT, or AVOID) might vary between APP and WMU 49 due to differences in proportional availability rather than moose behavior and we sought to verify this assumption prior to combining data from all moose in subsequent analyses.

**Thermoregulatory Habitat Use**

We used seasonal UDs 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, APP East Gate Station: 45° 31.8’N 78° 16.2’W; WMU 49, Beatrice Climate Station: 45° 8.4’N 79° 24.0’W; Fig. 2.1; Environment Canada 2008) and related corresponding temperatures in respective study areas with the GPS location data for the same time period for each moose. We used weather station data rather than temperatures collected from data loggers in our study area to provide a standard temperature metric for each study area and because our temperature sensors were not deployed concurrently with GPS collars. Within each season, moose relocations 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
relocation was recorded. Moose UDs were then calculated for each partition, so that each UD corresponded to utilization occurring above and below the UCL for each season. Thus, we obtained 4 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 4 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 by combining habitat categories that should provide similar thermal cover for moose (Stevens 2002). We pooled HEMLOCK stands into MIXED since HEMLOCK stands in the FRI were composed of as little as >40% hemlock and a mixture of hardwoods 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 since moose were likely foraging on aquatic plants or were partially submerged in water in all 3 categories. To attain approximate normal distributions of the response variables, UD proportions were arcsine square-root transformed prior to analysis. We used Wilk’s lambda criterion to test for overall significance (Quinn and Keough 2002). Analyses were performed using program R (v. 2.7.1, R Development Core Team 2008).
Thermal Cover

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 FRI stand validation and to reflect habitat combinations in the thermoregulatory habitat use analysis (CONIFER: \( n = 7 \); HARDWOOD: \( n = 26 \); MIXED: \( n = 26 \); WETLAND: \( n = 11 \)). We used temperature data collected on the data loggers from August 2007 (summer) and November and December 2007 (winter) and averaged temperatures within forest stands for each of 6 4-hour intervals (t1: 0000-0300; t2 = 0400-0700; t3: 0800-1100; t4: 1200-1500; t5: 1600-1900; t6: 2000-2300). We used one-way MANOVA to test for effects of habitat type on temperature differences throughout the day in each season. Post-hoc analysis included univariate tests with Bonferroni correction and pairwise comparisons using Tukey’s HSD test. All analyses were performed using program R (v. 2.7.1, R Development Core Team 2008).

Results

Landscape Habitat Use

We included relocation data from 36 radio-collared moose in our analysis (APP: \( n = 19 \) moose, WMU 49: \( n = 17 \) moose; \( \sim 302,000 \) GPS relocations). The average proportion of missed fixes per individual GPS collar was low in summer (5.0%; mean = 108 ± 271 (SD) relocations; \( n = 3,881 \) missed fixes) and winter (3.6%; mean = 164 ± 406 (SD) relocations; \( n = 5,903 \) missed fixes). Total number of relocations per moose used to
calculate kernels was large, but varied seasonally (summer: mean = 1,975 ± 421 (SD) relocations; n = 74,975 relocations; winter: mean = 4,287 ± 896 (SD) relocations; n = 160,275 relocations) due to differences in season length. Positional distance error for the GPS collars were assumed to be minimal given the results from a previous study that tested and used similar GPS collars in the same study area (mean = 33.8 ± 4.2 m (SD) for 2D fixes; mean = 14.4 ± 2.5 m (SD) for 3D fixes; A. J. Maxie and M. E. Obbard, unpublished data).

First, we classified moose habitat use for summer and winter with respect to availability in each study area into a categorical index representing patterns of overall use relative to availability (Table 2.2). Overall, most habitat types were used as expected (i.e., RANDOM) according to availability within the respective landscapes defined by the extent of moose relocations (Fig. 2.2.a and Fig. 2.2.b). However, probability of moose using either DEEP or SHALLOW WATER in summer and winter was considerably less than expected (AVOID) in both study areas and seasons (all \( P = 0; \) Table 2.2). Moose also tended to avoid HEMLOCK during the winter in WMU 49; the index of AVOID was not surprising given the low availability <1%, and 59% (n = 10) of moose were never relocated in HEMLOCK in WMU 49 (mean UD = 0%) indicating that this habitat type was heterogeneous across moose home ranges. Although moose use of HARDWOOD appeared high relative to all other habitat types in both seasons, the Index of Use was consistently RANDOM (\( P > 0.15; \) Table 2.2).

Indices of habitat use failed to correspond between study areas within the same season for only 1 habitat class in summer and 3 classes in the winter (see results below). Qualitatively, 1 of the categories differed markedly in availability between study areas
HEMLOCK: <1% in WMU 49 vs. 6.7% in APP). Where Index of Use did not correspond between study areas, differences were between RANDOM and AVOID or RANDOM and SELECT (i.e., means did not differ in opposite directions from proportional availability, e.g., SELECT in one area and AVOID in the other). Thus, we concluded differences in index of habitat use between APP and WMU 49 were small and largely due to differences in availability rather than moose behavior, and therefore we pooled moose from both study areas for all further analyses.

Thermal Cover

We tested for differences in ambient temperature among habitat types and detected variable temperature profiles through the day in both summer (Wilk’s lambda = 0.152, $F_{18,173} = 9.1$, $P<0.001$; Fig. 2.3) and winter (Wilk’s lambda = 0.283, $F_{18,173} = 5.4$, $P<0.001$; Fig. 2.4). All habitats exhibited high variation throughout the diurnal cycle, but there were only minor differences in temperature among habitat types. The sole exception was WETLAND, where summer temperature rose rapidly from early morning to the mid-afternoon peak ($\Delta \approx 10^\circ$C). The winter temperature profile exhibited a lesser cycle, with more stable temperatures at night and a smaller increase during the peak of the day; again, WETLAND habitat exhibited the most divergence from others, given that temperature in that habitat rose by $\approx 4^\circ$C through the morning-afternoon period compared to $\approx 2-3^\circ$C for CONIFER, HARDWOOD, and MIXED habitats.

Although temperatures during the summer were different among habitat types in each time interval (ANOVAs, 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 2.3). Similar patterns of habitat-specific temperature variability occurred during winter, except that temperatures differed among habitat classes in only 4 of 6 time intervals (ANOVAs, all \( P<0.001 \): 0000-0300 h (t1), 0400-0700 h (t2), 1200-1500 h (t4), and 2000-2300 h (t6). Again, most temperature differences were attributable to pairwise comparisons between WETLAND and other habitat classes (Tukey’s HSD, all \( P<0.005 \); Table 2.3). WETLAND was cooler in the earliest and latest periods of the day (t1: mean = -7.3 \pm 0.4°C (SD), t2: mean = -7.5 \pm 0.4°C (SD), and t6: mean = -6.5 \pm 0.4°C (SD); \( n = 11 \); Table 2.3), and warmer than all other habitats in the late afternoon (t4: mean = -1.9 \pm 1.2°C (SD); \( n = 11 \); Table 2.3).

Unexpectedly, all habitat classes greatly exceeded the 14°C threshold for much of the day (and partially during the night) in summer, except from approximately 0000-0700 when WETLAND and CONIFER dropped ~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). Thus, we conclude that although temperature was variable throughout the day in summer and winter, there was little difference in temperatures among our habitat classifications with the exception of WETLAND.

**Thermoregulatory Habitat Use**

Temperatures were sufficiently variable during our study to allow us to test for differences in habitat use above and below reported critical temperature thresholds. In summer, ambient temperature was >14°C for 65% (2,870 hours) of the study period; on average, it exceeded 14°C for a considerable portion of the day (15.6 \pm 6.2 (SD) hours; \( n \)
= 2,870 hours). The average magnitude of temperature (number of C°) greater than 14°C was 6.1 (± 3.9°C (SD); n = 2,870 hours). The greatest deviation above a temperature threshold we recorded was 19°C in the first week of August (2006). The longest duration (consecutive number of hours) temperatures remained above the threshold occurred in late July 2006 for 137 hours (~5.7 days). Ambient temperature exceeded the panting threshold (20°C) less frequently (30.9%; 1,365 hours); and was above the threshold for a shorter fraction of the day (7.4 ± 5.6 (SD) hours; n = 1,365 hours). Similarly, moose critical temperature thresholds were exceeded in winter, with temperatures >-5°C occurring 54.9% (5,392 hours) of the study period, and on average, temperature being above the threshold for roughly half of the day (13.2 ± 9.9 (SD) hours; n = 5,392 hours). The average magnitude of temperature (number of C°) greater than -5°C was 6.4 (± 4.9°C (SD); n = 5,392 hours). The greatest deviation above a temperature threshold we recorded was 29°C in late April 2007. The longest duration (consecutive number of hours) temperatures remained above the threshold in winter occurred in late April (2007) and lasted 472 hours (~19.5 days). Likewise, the winter panting threshold (0°C) was exceeded for 29.6% (2,902 hours) of the study period, and on average, temperatures were >0°C for the majority of daylight hours (7.1 ± 8.8 (SD) hours; n = 2,902 hours) (Environment Canada 2008).

Overall, we observed no differences in moose behavior relative to these temperature thresholds. Specifically, we found no difference in proportion of habitat types used above vs. below the published UCL either in summer (Wilk’s lambda = 0.745, $F_{5,31} = 2.1, P = 0.09$; Fig. 2.5) or winter (Wilk’s lambda = 0.729, $F_{5,31} = 2.3, P = 0.07$; Fig. 2.6). This finding was counter to the predicted increase in use of CONIFER (thermal
cover) and decrease in use of HARDWOOD (feeding areas) at high temperature. 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 actually increased \(<0.5\%\) in summer but decreased \(<0.5\%\) in winter. Similarly, we detected no differences in probability of habitat use above vs. below the reported panting threshold (summer: Wilk’s lambda = 0.751, \(F_{5,31} = 2.1, P = 0.10\); Fig. 2.5; winter: Wilk’s lambda = 0.756, \(F_{5,31} = 1.9, P = 0.11\); Fig. 2.6), with moose use of CONIFER increasing \(<2\%\) above the panting threshold in summer and winter. Correspondingly, use of HARDWOOD decreased by \(<1\%\) in both seasons. Thus, we conclude that moose behavior was consistent irrespective of temperature thresholds.

**Discussion**

Moose did not exhibit evidence for behavioral responses to thermal conditions that typically induce heat stress in our study. Overall, moose habitat utilization profiles closely corresponded to proportional availability of habitat classes in each study area, with deviations in only a few cases. This was not surprising given that moose are typically habitat generalists (Belovsky 1981), food and predation did not appear to be limiting (i.e. physical condition appeared good, and survival was high; D. L. Murray et al. unpublished data), and all of the habitat types were highly interspersed within the landscape (S. J. Lowe, unpublished data). Some observations were counter to our predictions; primarily, we anticipated moose would favor WETLAND and SHALLOW WATER habitats in the summer given the high accessibility of aquatic vegetation and the potential thermoregulation benefits of being submerged in water. Moose did not use WETLAND more than expected, and actually avoided SHALLOW and DEEP WATER
in the summer; this was likely due to the high availability of these 3 habitats. Although our index indicated moose tended to avoid DEEP and SHALLOW WATER, we recognize that our methods (both observational and analytical) could not rule out the possibility that moose selected land along lake shore edges in the summer to take advantage of the increased wind speed (and therefore increased convective cooling), and immediate escape route from predators vital to cows encumbered by newborn calves. We potentially underestimated use of these habitat classes because we defined use as a moose being physically located in a habitat type, rather than using a distance based approach to look for associations with habitats in addition to occupancy.

We also predicted moose would select CONIFER in the summer due to its potential for increased shade, and results of a previous study indicated mature conifers were used by moose as thermal shelters (Dussault et al. 2004), but our observations indicated that use was RANDOM. We were particularly intrigued by moose use of CONIFER stands in the summer (RANDOM) given that on average they appear to provide no thermal benefits over other habitat types. We speculate that use of CONIFER stands was due to their spatial juxtaposition in the landscape and specifically their proximity to WETLAND due to the proximity of cover to high quality forage. In fact, on average wetlands occurred closer to conifer stands than any other habitat type in both APP (168 ± 157 m (SD)) and WMU 49 (308 ± 265 m (SD)).

Habitat specific temperature profiles indicated that differences in ambient temperature among forested habitat types in our study area were minimal at the spatial resolution 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. Therefore at the macrohabitat (forest stand) scale, our results indicate that our study area is likely devoid of forested thermal shelters as defined by Renecker and Hudson’s (1986) seasonal temperature thresholds for moose. Intuitively, we would conclude that because we failed to detect substantial ambient temperature differences among forested habitat types we would also not expect moose habitat utilization to change relative to temperature. However, we would have expected that if movement and foraging were suppressed by heat stress, then proportion of habitat types would have reflected a difference due to moose being more sedentary (and thus not traveling freely amongst all habitat types). Our measurement of temperature does not accurately reflect thermal properties of the WETLAND habitat class since moose are likely to be partially submerged in water when located in WETLAND, but it does provide an informative comparison between open and closed canopy habitats. In addition, our thermal cover assessment may be too coarse because it does not account for the effects of wind and humidity (operative temperatures; see Schwab and Pitt 1991) which may alter microclimate temperatures. Our study design could have been improved by deploying multiple data loggers within the same forest stand to account for heterogeneity in temperature due to variability in canopy closure; our current measurement reflects assessment under shade in all stands (with the exception of WETLAND) and thus may not be representative of stand-level averages.

From a behavioral perspective, individuals respond to daily and seasonal pressures by making frequent tradeoffs 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 limiting
fitness, then we expect habitat use patterns to be influenced by temperature, especially
when it exceeds upper critical limits and induces heat stress. Therefore, we expected
moose would suppress foraging activities to seek out the densest shade available
(presumably in conifer stands), and habitat utilization patterns should fluctuate
accordingly. Surprisingly, moose in our study area did not alter habitat use patterns
relative to reported thermoregulation thresholds in summer or winter (Renecker and
Hudson 1986); probability of use of each habitat type did not change when compared
above vs. below the critical threshold. Even when we tested the more conservative
critical temperature (panting threshold) we failed to detect a change in habitat utilization
patterns, suggesting that moose in our study area did not demonstrate behavioral
responses to ambient conditions.

Empirical evidence reported for moose behavioral responses to summer thermal
conditions is generally consistent across moose range in North America. Moose in the
boreal forest in Quebec, Canada 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, Canada selected mature forest to relieve heat stress when operative
temperatures exceeded critical limits. Additionally, moose in Alberta, Canada reduced
both energy expenditure and respiration rates by bedding in wet meadows in the summer
(Renecker and Hudson 1990). However, our results did not concur with reported
findings of previous studies; we failed to detect a relationship between habitat utilization
and temperature in our study area in summer or winter at the thresholds we tested.
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 were above the critical threshold ~33% of the day. Likewise, temperatures in Dussault et al’s. (2004) study exceeded thermal limits for heat stress in winter, yet they failed to detect evidence of thermal shelter selection. In fact, their results were counter-intuitive with moose increasing activity levels in spring with warmer temperatures.

Previously reported temperature thresholds for moose may be inaccurate due to small sample size and use of captive individuals (n = 2 female moose; Renecker and Hudson 1986). We suspect that the 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 critical aspects of temporal temperature patterns that could potentially influence the extent of the severity of heat stress in moose. Specific aspects warranting further testing include duration of consecutive time and magnitude of temperature above upper critical limits. 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 above a certain temperature to induce heat stress, and it follows that there may be a substantial interaction with the rate of change in ambient temperature as well as the magnitude on initiating heat stress (and in determining how long it is sustained) in moose. Additionally, acclimation time may play a key role in determining if moose elicit heat stress responses. Furthermore, moose may be responding to temperature at a smaller spatial scale (e.g., microclimate) making it difficult to discern patterns of behavioral thermoregulation responses at a macrohabitat
scale. For example, even with bihourly GPS fixes over a long time period, the scale and accuracy of currently available habitat maps is coarse relative to the data collected on animal locations; therefore our ability to relate the appropriate scale of habitat data is limited. To our knowledge, no one has quantified moose habitat use at finer scales (e.g., bed sites), especially as it relates to reduction in heat stress.

We explored the possible effects of snow depth, a potential confounding factor, in contributing to a lack of detectable response in moose habitat use relative to ambient temperature in winter. Moose movement (and therefore habitat use behavior) may be suppressed due to increased energy demands of locomotion in deep snow (Renecker and Schwartz 1998). Reported limiting snow depths ranged from 50-90 cm (Coady 1974, Kelsall 1969, Geist 1998, Thompson and Vukelich 1981). We collected daily snow depth data from the Environment Canada weather station at the APP East Gate (45° 31.8’N 78° 16.2’W; Environment Canada 2008) and calculated the amount of time in each winter season that snow depths exceeded the lowest reported snow depth (50 cm; Geist 1998) to provide the most conservative estimate. Throughout our study, snow depths rarely exceeded the lowest snow depth threshold for impeded movement by moose with the exception of 2006, during which moose were only monitored from mid-January on. Overall, snow depth was >50 cm for 42.5% (51 days) in 2006, 0% (0 days) in 2007, and 5.4% (9 days) in 2008. Additionally, preliminary assessment of proportional habitat use showed no difference in winter habitat use among the 3 years of our study (S. J. Lowe, unpublished data). Thus, we discounted snow as a possible factor restricting moose habitat use in the winter.
Is climate change likely to impact the geographic distribution of moose along the southern periphery of the range in central Ontario? Intuitively, we would expect that a large northern ungulate with low tolerance for high ambient 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 can suppress foraging time and consequently cause weight loss during the summer, the season traditionally reserved for weight gain to provide energy through the winter (Schwartz and Renecker 1998). If habitat conditions were poor enough, and if other factors were concurrently limiting (i.e., predation, parasitism, etc.), then we would expect individual fitness to decrease and eventually population decline to follow, such as the example of the moose population decline reported in north western Minnesota (Murray et al. 2006). The role of climate in inhibiting geographic ranges often assumes causality and ignores interactions with other abiotic and biotic factors (Gaston 2003). Furthermore, many species have the physiological capacity to withstand conditions typical of areas beyond their present geographic range, but these tolerances frequently remain untested experimentally in favor of characterizing the environmental conditions where they occur with anything outside those limits being deemed intolerable (Gaston 2003). Because we ultimately found no evidence of moose exhibiting behavioral responses to thermal stress, we discount the role of climate 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, and consideration of alternative scales of habitat use (microhabitat), and reduction in overall activity levels is warranted in future research.
We recommend a rigorous assessment of critical temperature thresholds on free ranging moose including males, which are potentially more vulnerable to heat stress due to their larger body size. Furthermore, we suggest temporal components such as duration and magnitude of high temperatures, as well as effects of acclimation time, should be tested experimentally to improve understanding of heat stress tolerance in moose.
Table 2.1. Description of dominant tree species within combined habitat classes in the Forest Resource Inventory (FRI) data layer for the Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU 49) study areas, central Ontario, Canada.

<table>
<thead>
<tr>
<th>Habitat Class</th>
<th>Dominant Tree Species¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>HARDWOOD</td>
<td>Sugar maple⁹, American beech¹⁰, Yellow birch¹¹, Red maple¹², Red oak¹³, Poplar¹⁴, White birch¹⁵</td>
</tr>
<tr>
<td>MIXED</td>
<td>Poplar, Red maple, White birch, Balsam fir¹⁶, Sugar maple, Cedar¹⁷, Jack pine¹⁸, Black ash¹⁹</td>
</tr>
<tr>
<td>CONIFER</td>
<td>Red pine¹⁰, White pine¹⁶, Poplar, White birch, Red oak, Balsam fir Black spruce¹⁸, White spruce¹⁶, Cedar, Jack pine, Larch¹⁹</td>
</tr>
<tr>
<td>HEMLOCK</td>
<td>Eastern hemlock¹⁰, Yellow birch, Sugar maple</td>
</tr>
<tr>
<td>WETLAND</td>
<td>Brush and alder¹⁰, Open muskeg, Treed muskeg</td>
</tr>
<tr>
<td>DEEP WATER</td>
<td>Water &gt;100 m from shoreline</td>
</tr>
<tr>
<td>SHALLOW WATER</td>
<td>Water &lt;100 m from shoreline</td>
</tr>
<tr>
<td>OTHER</td>
<td>Roads, Developed or agricultural land, Exposed rock (sparsely vegetated), Unclassified habitat</td>
</tr>
</tbody>
</table>

¹See Maxie et al. *in press* for complete descriptions of habitat classes

¹Acerr saccharum, ²Fagus grandifolia, ³Betula alleghaniensis, ⁴Acer rubrum, ⁵Quercus rubra, ⁶Populus spp., ⁷Betula papyrifera, ⁸Abies balsamea, ⁹Thuja occidentalis, ¹⁰Pinus banksiana, ¹¹Fraxinus nigra, ¹²Pinus resinosa, ¹³Pinus strobus, ¹⁴Picea mariana, ¹⁵Picea glauca, ¹⁶Larix laricina, ¹⁷Tsuga canadensis, ¹⁸Alnus spp.
Table 2.2. Moose habitat use and availability in the Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU 49) study areas in winter and summer. The Index of Use corresponds to results of a one-sample t-test between use and availability; where RANDOM: P>0.05; AVOID: P<0.05, with use being less than available; SELECT: P<0.05, with use being greater than available.

<table>
<thead>
<tr>
<th>Study Area</th>
<th>Habitat Type</th>
<th>Summer</th>
<th>Winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>APP</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer</td>
<td>RANDOM</td>
<td>0.10</td>
<td>1.29</td>
</tr>
<tr>
<td>Deep Water</td>
<td>AVOID*</td>
<td>-14.66</td>
<td>-44.82</td>
</tr>
<tr>
<td>Hemlock</td>
<td>RANDOM</td>
<td>0.97</td>
<td>-1.41</td>
</tr>
<tr>
<td>Hardwood</td>
<td>RANDOM</td>
<td>-0.02</td>
<td>-3.68</td>
</tr>
<tr>
<td>Mixed</td>
<td>AVOID</td>
<td>-3.09</td>
<td>-4.82</td>
</tr>
<tr>
<td>Other</td>
<td>AVOID</td>
<td>-4.38</td>
<td>-3.88</td>
</tr>
<tr>
<td>Shallow Water</td>
<td>RANDOM</td>
<td>-0.24</td>
<td>-6.95</td>
</tr>
<tr>
<td>Wetland</td>
<td>RANDOM*</td>
<td>-4.01</td>
<td>-7.88</td>
</tr>
<tr>
<td>WMU 49</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer</td>
<td>RANDOM*</td>
<td>-0.36</td>
<td>-0.36</td>
</tr>
<tr>
<td>Deep Water</td>
<td>AVOID*</td>
<td>-49.07</td>
<td>-11.96</td>
</tr>
<tr>
<td>Hemlock</td>
<td>RANDOM*</td>
<td>-2.29</td>
<td>-5.93</td>
</tr>
<tr>
<td>Hardwood</td>
<td>RANDOM</td>
<td>1.45</td>
<td>0.71</td>
</tr>
<tr>
<td>Mixed</td>
<td>AVOID*</td>
<td>0.12</td>
<td>0.488</td>
</tr>
<tr>
<td>Other</td>
<td>AVOID</td>
<td>-3.67</td>
<td>-1.96</td>
</tr>
<tr>
<td>Shallow Water</td>
<td>RANDOM</td>
<td>-1.10</td>
<td>-0.289</td>
</tr>
<tr>
<td>Wetland</td>
<td>RANDOM</td>
<td>0.20</td>
<td>0.002</td>
</tr>
</tbody>
</table>

* Indicates discrepancy in Index of Use classification between study areas (within seasons)
Table 2.3. Pairwise comparisons (Tukey’s HSD) in temperature among habitat types in summer and winter; differences within time intervals (T1: 0000-0300; T2 = 0400-0700; T3: 0800-1100; T4: 1200-1500; T5: 1600-1900; T6: 2000-2300) represent C° difference in habitat specific temperature averages for each pairwise comparison performed for summer (August 2007) and winter (November and December 2007).

<table>
<thead>
<tr>
<th>Time Interval</th>
<th>T1</th>
<th>T2</th>
<th>T3</th>
<th>T4</th>
<th>T5</th>
<th>T6</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pairwise Comparison</strong></td>
<td><strong>Difference (°C)</strong></td>
<td><strong>Difference (°C)</strong></td>
<td><strong>Difference (°C)</strong></td>
<td><strong>Difference (°C)</strong></td>
<td><strong>Difference (°C)</strong></td>
<td><strong>Difference (°C)</strong></td>
</tr>
<tr>
<td><strong>Summer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>hardwoods-conifer</td>
<td>1.3*</td>
<td>1.8*</td>
<td>0.7</td>
<td>0.3</td>
<td>0.7</td>
<td>0.5</td>
</tr>
<tr>
<td>mixed-conifer</td>
<td>1.1*</td>
<td>1.4*</td>
<td>0.4</td>
<td>0</td>
<td>0.3</td>
<td>0.5</td>
</tr>
<tr>
<td>wetland-conifer</td>
<td>1.4*</td>
<td>0.7</td>
<td>3.4*</td>
<td>2.8*</td>
<td>0.9</td>
<td>1.8*</td>
</tr>
<tr>
<td>mixed-hardwoods</td>
<td>0.2</td>
<td>0.4</td>
<td>0.3</td>
<td>0.3</td>
<td>0.4</td>
<td>0</td>
</tr>
<tr>
<td>wetland-hardwoods</td>
<td>2.7*</td>
<td>2.5*</td>
<td>2.7*</td>
<td>3.2*</td>
<td>1.6*</td>
<td>2.3*</td>
</tr>
<tr>
<td>wetland-mixed</td>
<td>2.4*</td>
<td>2.1*</td>
<td>3.0*</td>
<td>2.9*</td>
<td>1.2*</td>
<td>2.3*</td>
</tr>
<tr>
<td><strong>Winter</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>hardwoods-conifer</td>
<td>0.3</td>
<td>0.4</td>
<td>n.s</td>
<td>0.6</td>
<td>n.s.</td>
<td>0.1</td>
</tr>
<tr>
<td>mixed-conifer</td>
<td>0.2</td>
<td>0.3</td>
<td>n.s</td>
<td>0.2</td>
<td>n.s.</td>
<td>0.2</td>
</tr>
<tr>
<td>wetland-conifer</td>
<td>0.8*</td>
<td>0.6</td>
<td>n.s</td>
<td>1.5*</td>
<td>n.s.</td>
<td>0.8*</td>
</tr>
<tr>
<td>mixed-hardwoods</td>
<td>0</td>
<td>0.1</td>
<td>n.s</td>
<td>0.4</td>
<td>n.s.</td>
<td>0</td>
</tr>
<tr>
<td>wetland-hardwoods</td>
<td>1.0*</td>
<td>1.0*</td>
<td>n.s</td>
<td>0.9*</td>
<td>n.s.</td>
<td>0.9*</td>
</tr>
<tr>
<td>wetland-mixed</td>
<td>1.0*</td>
<td>0.9*</td>
<td>n.s</td>
<td>1.3*</td>
<td>n.s.</td>
<td>0.9*</td>
</tr>
</tbody>
</table>

*indicates significant difference ($P<0.01$)

n.s. indicates nonsignificant ANOVA, no Tukey's HSD performed
Fig. 2.1. Location of study areas in Algonquin Provincial Park (APP) and Wildlife Management Unit (WMU) 49 in central Ontario, Canada. The 2 study areas are hatched. Environment Canada weather station locations are indicated by a star.
Fig. 2.2.a. Proportional summer habitat use by moose in Algonquin Provincial Park (APP) \((n = 19)\) and Wildlife Management Unit 49 (WMU 49) \((n = 17)\) in central Ontario, Canada, compared to proportional study area availability. Proportion of habitat use represents mean Utilization Distribution among moose in summer, and proportion of habitat available represents the proportional availability within the study area. Error bars represent ± 1 SE.
Fig. 2.2.b. Proportional winter habitat use by moose in Algonquin Provincial Park (APP) 

\( n = 19 \) and Wildlife Management Unit 49 (WMU 49) \( n = 17 \) in central Ontario, 

Canada, compared to proportional study area availability. Proportion of habitat use 

represents mean Utilization Distribution among moose in winter, and proportion of 

habitat available represents the proportional availability within the study area. Error bars 

represent \( \pm 1 \ SE \).
Fig. 2.3. Summer mean temperatures among habitat classes throughout the day. Time intervals (T1: 0000-0300; T2: 0400-0700; T3: 0800-1100; T4: 1200-1500; T5: 1600-1900; T6: 2000-2300) represent habitat specific averages for summer (August 2007); error bars represent ± 1 SE of temperature means.
Fig. 2.4. Winter mean temperatures among habitat classes throughout the day. Time intervals (T1: 0000-0300; T2: 0400-0700; T3: 0800-1100; T4: 1200-1500; T5: 1600-1900; T6: 2000-2300) represent habitat specific averages for winter (November and December 2007); error bars represent ± 1 SE of temperature means.
Fig. 2.5. Probability of summer habitat use by moose (n=36) in central Ontario, Canada relative to the reported upper critical temperature limit threshold (14°C) for thermoregulation, and the reported panting temperature threshold (20°C) for moose in summer. Probability of use represents mean Utilization Distribution (UD) for specified temperature category; error bars represent ± 1 SE.
Fig. 2.6. Probability of winter habitat use by moose (n=36) in central Ontario, Canada relative to the reported upper critical temperature limit threshold (-5°C) for thermoregulation, and the reported panting temperature threshold (0°C) for moose in winter. Probability of use represents mean Utilization Distribution (UD) for specified temperature category; error bars represent ± 1 SE.
Chapter 3

General Conclusion

There is considerable interest in the study of factors and processes driving limitations in the geographic range of species (Gaston 2003, Krebs 2001, Parmesan et al. 2005). Frequently, scientists and managers want to determine potential available habitat for population expansion or reintroductions, or would like to anticipate potential distribution shifts near range peripheries. In light of ongoing climate change, knowing how a species responds to temperature, and linking these factors to population level processes is important, and relies on rigorous assessment of habitat requirements and behavioral mechanisms for coping with heat stress. Linking individual behavior and fitness to long-term population scale processes is difficult in ecological studies due to their complex nature, yet it plays a vital role in understanding the synergistic effects within a system and is poorly understood in many organisms. Furthermore, understanding what species are most vulnerable to effects of climate change can help direct research and management efforts appropriately and efficiently to achieve conservation goals.

Climate is only one of many factors that contribute to geographic range limits of species; however, it is likely the most studied due to the widespread nature of global warming concerns and the potential for it to impact species at a rapid rate, as well as the readily available nature of climate and species occupancy data (Gaston 2003, Parmesan et al. 2005). In anticipation of globally rising temperatures, considerable research has been focused on potential effects on population abundance and spatial distributions of some
species, especially for those already imperiled by confounding factors. I sought to
determine if temperature was acting as a limiting factor for the geographic range of
moose (Alces alces) along the southern range extent. The circumpolar distribution of
moose exemplifies a species physiologically adapted to cold climates (Telfer 1984).
Although largely unaffected by ambient temperatures at their lower critical limits
(approximately -30°C), thermoregulation was suggested to be vital for moose in summer
and winter when ambient temperatures exceed their upper critical limits of 14°C and -
5°C, respectively (Renecker and Hudson 1986). Murray et al. (2006) suggested that
moose in northwestern Minnesota, and potentially across their southern distribution in
North America, are experiencing numerical decline and facing possible extirpation as a
result of increasing temperatures, coupled with proximate factors like malnutrition and
parasitism. Yet, this correlation between climate and population decline lacked a clear
linkage between inclement weather and moose behavioral responses; such responses are
predicted if moose in the southern range have adaptive behaviors that improve their
fitness. I selected moose for this research because of all northern ungulates, they are
likely the most susceptible to heat stress, and thus potentially the most vulnerable to
effects of climate change. Research has already shown that climate may be limiting for
moose populations in some parts of their southern range (Murray et al. 2006). However,
moose range is also expanding southward in other areas of their southern distribution
(New England; Degraff and Yamasaki 2001) where climate should also be limiting to the
spatial expansion of moose populations. This discrepancy in range changes warrants a
critical assessment of the factors attributable to limiting moose range, especially along
the southern periphery.
My results suggest that moose did not alter habitat use behavior when temperatures indicated that they should have been heat stressed. The lack of habitat selection responses to ambient temperature conditions at the thresholds I considered suggests that this population is potentially more resilient to high temperatures than previously speculated. My results also showed minimal differences in temperature among habitat types at the macrohabitat scale, meaning that my classification of forest stands composed of different tree species did not represent a clear gradient in quality of thermal cover for moose as expected. Initially, the lack of behavioral response of moose to ambient temperatures exceeding their upper critical limits in summer and winter was surprising. I would expect in my system where temperatures were potentially more limiting to detect a stronger response than previous studies located further north in the geographic range of moose. Additionally, my analytical approach was robust because it did not assume any particular habitat classes provided thermal cover, and tested for changes in the overall habitat utilization profiles above vs. below critical thresholds.

In a previous study, moose used mature conifer stands when they were heat stressed likely to avoid the intense solar radiation in the clear cut stands present in the intensively harvested landscape (Dussault et al. 2004). Based on the Dussault et al. (2004) study, I expected to observe a difference in proportion of habitat types used if moose were truly heat stressed in my system. However, my results indicated that moose did not alter habitat utilization patterns relative to ambient temperature at the thresholds I tested. Several factors may contribute to the different results observed for moose behavioral responses to thermal conditions. The thresholds that have functioned as the standard for reference to heat stress in moose may be inaccurate due to a small sample
size and use of captive animals, especially when applied to free ranging moose. Moose may also exhibit more prominent differences in habitat use in response to these temperature thresholds in areas with more pronounced temperature differences among dominant habitat types. Furthermore, moose may be able to compensate for the higher energy demand and offset potential energy deficiencies caused by heat stress by consuming higher quantities of forage (Dussault et al. 2004).

**Future Research**

My research contributes to the understanding of potential limiting factors to the geographic range of moose by suggesting that temperature in and of itself does not seem to be negatively affecting moose near the southern limit of their range in central Ontario. Furthermore, I demonstrated how hypotheses about large scale patterns (geographic range limits) can be tested from a behavioral perspective at the scale of the individual animal. Accordingly, the next step is to link my results with population-scale processes such as survival and fecundity to inform predictive models on effects of individual behavior on population persistence. However, I caution that the foundation of the underlying question (determination of upper critical temperature thresholds) needs to be revisited before stronger conclusions are drawn regarding the thresholds I tested.

Although I investigated only part of the phenomenon of behavioral thermoregulation in moose, I highlight the need for further research of this aspect of moose ecology. First, I recommend rigorous experimental testing of the upper critical limits in free ranging moose. Without a reliable threshold, there is potential to make false conclusions regarding moose behavior relative to ambient conditions. Secondly, limited
attention has been given to understanding the potential thermoregulatory benefits of use of aquatic habitats by moose. Most studies avoid this question. For example, data collected from aquatic habitats tends to be removed from thermal shelter analyses (e.g., Dussault et al. 2004, see also Schwab and Pitt 1991). Moose need to replace sodium used for reproduction, hair growth, and lactation (Belovsky and Jordan 1981). The utility of aquatic resources as a critical food source and thermal shelter is inherent, but disregarding their use in habitat use analyses may alter interpretations of behavioral thermoregulation. I included aquatic habitats in my analysis, but failed to detect a relationship with temperature, and overall moose actually avoided both water classes when compared to the proportional availability on the landscape. Nonetheless, water can potentially lower body temperature at a rapid rate, and even brief exposure could provide thermal relief for moose.

Another area of deficiency in the current literature is the effect of spatial and temporal scale for addressing the behavioral thermoregulation hypothesis in moose. For example, if moose initially select habitat at the coarsest spatial scale of resource selection (species range within a continent), then we may fail to detect changes if we analyze only at the smaller scale (within individual moose home ranges). Conversely, analyzing habitat use patterns at the macrohabitat scale within the home range may be too coarse; moose may seek thermal cover under a small patch of trees or may bed in the snow to aid in reduction of heat stress. Similarly, moose may be responding to ambient conditions at different temporal scales than have previously been tested. Specifically, previous research has only assessed behavioral responses within a seasonal scale; there may be responses occurring within diurnal cycles that have yet to be investigated. Future
research should attempt to fully explore microhabitat use and smaller scale effects such as convective and conductive cooling in microclimates, and additionally investigate behavior within the diurnal cycle. An alternative approach may be to simply monitor and observe what happens in the future and take advantage of a large-scale “experimental” approach by following a population through the course of a natural experiment (Parmesan et al. 2005). If moose range recedes along the southern periphery as temperatures warm, and other limiting factors remain unchanged, it might be reasonable to assume that moose do not possess sufficient behavioral responses to ameliorate heat stress sufficiently to persist.

In summary, my results indicate that moose may be more resilient to heat stress than previously suggested. Moose did not exhibit behavioral thermoregulation responses in the form of habitat use at the scale and thresholds I tested, but because the thresholds I tested may have been overly conservative, rigorous investigation of more liberal thresholds is warranted. If the reported thresholds are shown to be accurate, this may indicate that moose populations along the southern periphery of the range in Ontario are limited by factors rather than temperature induced heat stress, and research efforts should be directed accordingly.
Literature Cited


ESRI. 2004. Environmental Systems Research Institute, Inc., Redlands, California, USA.


