EFFECTIVE TEMPERATURE DIFFERENCES AMONG COVER TYPES IN NORTHEAST MINNESOTA

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ABSTRACT: Climate is probably one of the ultimate influences on the southern boundary of moose (*Alces alces*) distribution because moose are sensitive to warm temperatures in both summer and winter. In 4 different cover types in northeastern Minnesota we compared ambient temperatures to black globe temperatures that measures mean radiant temperature of the environment. The 4 cover types were mixed forest, treed bogs, coniferous forest, and deciduous forest that comprised ~85% of home ranges of radio-collared moose in northeastern Minnesota. Ambient temperature measurements taken from a weather station within the study area exceeded assumed physiological thresholds of 14 and 20° C for 50 and 33% of the study period, respectively. Black globe temperatures varied among cover types and temperature differences increased within cover types as ambient temperature increased. The greatest difference between deciduous and conifer cover was 2° C in black globe temperature and occurred during warm periods when skies were clear. The biological significance of these temperature differences is not clear and suggests the presence of alternative cooling mechanisms of cover types, such as water and possibly soil and duff layers acting as heat sinks. Use of these potential alternative cooling mechanisms should be considered in future research.

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Key words: Alces alces, cover type, home range, Minnesota, moose, temperature.

Food supply, habitat composition, and climate all influence the distribution of moose. Climatic influences on moose survival and distribution may be most pronounced and play a larger role in limiting populations near the southern edge of the range (Kelsall and Telfer 1974). Regions where temperatures frequently exceed 27° C during summer do not support moose populations unless shaded areas, rivers, or lakes are present (Demarchi 1991). As a circumboreal species, moose are well adapted to cold but are intolerant of warm temperatures and show both physiological and behavioral responses in warm weather (Renecker and Hudson 1986, 1990).

Temperature thresholds of 14 and 20 C that induce physiological responses by moose are from data collected on 2 captive moose in Alberta that increased respiration rate when exposed to ambient temperature>14°C and be-

gan open-mouthed panting when temperature exceeded 20° C (Renecker and Hudson 1986). These thresholds were accepted and applied to free-ranging animals uncritically for more than 20 years; for example, they were used as thresholds in measuring moose response to heat in the boreal forest of Quebec (Dussault et al. 2004). Recently, these thresholds were tested with thermometer data loggers deployed in cover types used by moose in southeastern Ontario. Because ambient temperature frequently exceeded these thresholds, Lowe et al. (2010) concluded that they were too low or not applicable for southeastern Ontario.

However, the literature indicates that moose do respond to high ambient temperatures. In warmer periods during winter and summer, forest cover types within home ranges have lower temperatures and reduced solar radiation compared to open habitats (Black

et al. 1976, Schwab and Pitt 1991, Demarchi and Bunnell 1993). Denser canopies of mature forests were used by moose during hot temperatures in British Columbia (Demarchi and Bunnell 1995), and behavioral responses in summer include shifting activity to night and early morning hours and using cooler forest cover types (Dussault et al. 2004, Broders et al. 2011). Unexpectedly, use of cover type during both summer and winter by moose wearing GPS radio-collars in southeastern Ontario did not change with increasing temperatures (Lowe et al. 2010). However, temperature differences among forest cover types were <2°C, implying that different forest cover types may not have varied in quality as thermal refuge.

Further work is required to resolve these conflicting results. If moose are sensitive to high ambient temperatures, then it follows that moose should exhibit thermoregulatory behavior, especially at the southern edge of their range such as in northeastern Minnesota and southeastern Ontario. In this study we compared the length of time that temperature was above the 14 and 20° C thresholds during summer in northeast Minnesota, and used black globe thermometers to compare the thermal environment among forest cover types during variable weather conditions. Our objective was also to establish baseline information about how these cover types reflect different thermal conditions during summer.

STUDY AREA

This study was conducted in Lake County in the arrowhead region of northeast Minnesota that has a humid continental climate with severe winters and short, warm summers (Frelich 2002). Precipitation is moderate with an average of 65-75 cm during spring, summer, and fall. Average snowfall along the north shore of Lake Superior in northeast Minnesota is about 180 cm annually with snow cover usually present from December-April. The average July temperature is ~17.5° C and the average January temperature is -17° C (NOAA 2009). Topography of the region is relatively flat with elevation 460-610 m above sea level.

Northeast Minnesota has near-boreal forests, which are the southern extensions of boreal forest from Canada that also contain stands of more southern species not typical of true boreal forests (Frelich 2002). These forests are classified into 5 main stand types: 1) fir-birch (Abies balsamea, Betula papyrifera) forests found on good soils, 2) jack pine (Pinus banksiana) and black spruce (Picea mariana) on coarse, shallow soils, 3) red maple (Acer rubrum), aspen (Populus tremuloides), birch, and fir in moist areas, 4) red pine (Pinus resinosa) on shallow rocky soils, and 5) birch and white pine (Pinus strobus) along lakes and streams. Conifer swamps dominated by tamarack (Larix laricina) and black spruce are also present.

METHODS

We measured temperature in 4 different forest cover types throughout the spatial extent of 95% kernel home ranges of VHF-collared moose in northeast Minnesota (Moen et al. 2011). Capture protocols and survival data for the VHF project are presented elsewhere (Lenarz et al. 2009, 2010). Random points along roads and trails within the home ranges were generated using ArcView 3.3 with a 200 m buffer.

Black globe temperature data loggers were used to determine differences in radiant heat load of local environments. Black globe thermometers measure the thermal environment by incorporating ambient temperature, wind velocity, and radiant energy (Bond and Kelly 1955). Black globe temperature data loggers were placed >25 m and <200 m from road edges within the study area. Black globes were constructed from 15 cm diameter copper bulbs painted matte black. HOBO[®] Pendant or Pro v2 Temperature-Relative Humidity Data Loggers were attached so sensors hung in the center of each globe.

HOBO Pendant temperature data loggers measure air temperature with an accuracy of $\pm 0.47^{\circ}$ C from -20 to 70°C, and HOBO Pro v2 temperature data loggers measure air temperature with an accuracy of $\pm 0.02^{\circ}$ C from 0 to 50° C. Temperature data loggers were synchronized to begin taking temperature samples at 6 minute intervals for 120 days during summer. Stored temperature readings were downloaded every 30 days to ensure data loggers were working properly and that data were not lost.

ArcView 3.3 and Land Use Land Cover LANDSAT Thematic Mapper (TM) images were used to identify and locate forest cover types that potentially offered thermal relief within the home ranges. Land Use Land Cover (LULC) satellite imagery was used to estimate cover type frequency and distribution in the study area. It is a raster dataset with 30 m resolution, >95% classification accuracy, and 16 defined cover types (Minnesota Department of Natural Resources [MNDNR] 2007). The 4 cover types were mixed forest consisting of approximately 50% mature deciduous and 50% mature coniferous canopy $(41 \pm 1\%)$, wetlands consisting of treed bogs $(18 \pm 2\%)$, coniferous forest (19 \pm 1%), and deciduous forest (3 \pm 1%); together they composed $80 \pm 1\%$ ($\overline{x} \pm$ SE) of the 95% kernel home ranges.

Forty temperature data loggers were placed within the 4 cover types (10 per cover type); one at each of the random points generated using ArcView 3.3 (Fig. 1). Black globes were secured to the trunk of a tree by a steel eye-bolt attached 75 cm above the ground, the approximate shoulder height of a moose while lying down, and extended 15 cm from the tree. Black globes were attached by the eye-bolt extending from the top of the black globe to the steel bolt extending from the tree. All globes were attached to the northeast side of the trees for standardization and to reduce the chance that direct sunlight would be shining on the black globes during the warmest parts of the day. Topographic and aspect variation were controlled for by placing black globes at flat locations within the defined cover types.

We measured the amount of time when ambient temperature exceeded 14 and 20° C. We also defined a hot day when maximum ambient temperature reached or exceeded 24.4°C, the average maximum daily temperature during July (NOAA 2009), to determine if there were greater differences between cover types when ambient air temperature exceeds normal conditions experienced by moose in northeast Minnesota. Cloudy days were defined as days when the cloud cover index was \geq 7, and clear days were defined as days when the cloud cover index was ≤ 3 (Minnesota Climatology Working Group 2010); the cloud cover index is a scale ranging from 1-10. Ambient air temperature and cloud cover data for the region were retrieved from NOAA and the Minnesota State Climatology archived data for the Isabella weather station located within the study area (Fig. 1).

Temperature data were analyzed with repeated measures ANOVA using Statistix (version 9, Analytical Software, Boca Raton, Florida). Bonferroni comparisons were used to test for differences among cover types; significance level was set at P = 0.05 for all tests. Sub-samples of the data were analyzed to determine the degree to which cover type temperatures differed due to time of day, season, and climatic events such as hot, cloudy, clear, and hot/clear days.

RESULTS

Ambient temperature exceeded 14° C for 50% of the time at the weather station in Isabella from 15 June-15 October, 2009 (Fig. 1). On days when ambient temperature exceeded 14°C, it typically remained there for about 15.3 h; the longest period was 120 consecutive hours (5 days) during August. During those 5 days, ambient temperature was >20° C between 08:00-20:00 hr, with a mean temperature of 24.5 \pm 0.5° C ($\bar{x} \pm$ SE).

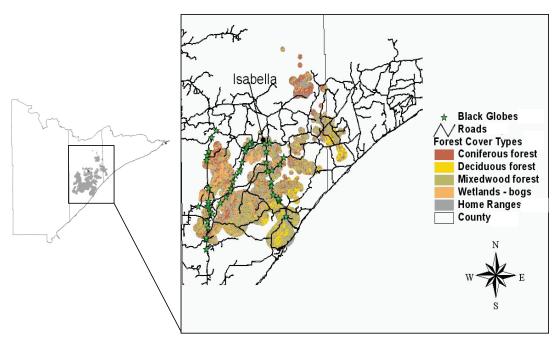


Fig. 1. Locations of temperature data logger in northeast Minnesota. Darker gray areas seen in the small insert of northeast Minnesota indicate 95% kernel home ranges of VHF-collared moose. Forest cover types are from Land Use Land Cover coverage classifications. The ambient temperatures used to compare with black globe temperatures were collected at a weather station in Isabella, Minnesota.

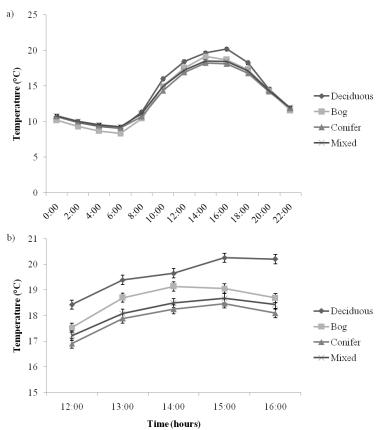
Ambient temperature exceeded 20° C for 33% of the study period when the mean temperature was $23.0\pm0.09^{\circ}$ C. On average, temperatures remained above 20° C for 6 ± 0.49 h, with the longest continuous period being 18 h.

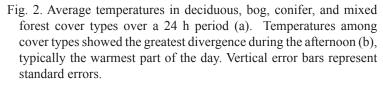
Highest black globe temperatures were recorded in the afternoons with the greatest difference in temperature between coniferous and deciduous cover types ($17.9 \pm 0.4^{\circ}$ C vs. $19.6 \pm 0.4^{\circ}$ C, $\bar{x} \pm$ SE; $F_{3,39} = 4.47$, P < 0.001). Black globe temperatures in mixed and bog cover types were intermediate between deciduous and conifer cover types, with the treed bog cover type having slightly cooler temperatures at night (Fig. 2).

As ambient temperature increased, differences in temperature among cover types were greater, with temperature differences from 1.1° C (above 14° C) to 2.1° C (above 24.4° C). The temperature difference between cover types was greatest between deciduous and coniferous cover types when ambient temperature was >14° C (Table 1). During 3 separate 11 hour periods (2 in August, 1 in June) when ambient temperature was >24.4°C, temperature differences between the deciduous and conifer cover types ranged from 1.5-2.4° C, with warmer periods resulting in larger differences in temperature. Temperature differences between cover types were greatest during the afternoons ($F_{3.39}$ = 4.59, *P* <0.009) (Fig. 2).

Differences in temperature between cover types were smaller on cloudy days compared to clear days. On clear days (cloud cover index <3) deciduous and bog cover types had the largest difference in temperature (Table 1). When we restricted the sampling to afternoon (12:00-16:00 hr), the deciduous cover type again had the highest temperature while the conifer cover type had the lowest temperature (Fig. 3, Table 1). The difference was greatest during the afternoons of days when temperature was >24.4 ° C without cloud cover (Fig. 3, Table 1).

On cloudy days (cloud cover index >7) there were smaller differences in temperature





between cover types, although the deciduous cover type still had the highest temperatures and the coniferous cover type had the lowest temperatures. When the sampling period was restricted to the afternoon, differences became greater once again (Fig. 3, Table 1). Days when ambient temperature exceeded 24.4° C were not cloudy.

DISCUSSION

The uncritical acceptance of 14 and 20°C thresholds for moose thermoregulatory response was recently raised because of temperatures within moose range in southeast Ontario (Lowe et al. 2010). Summer ambient temperatures in cover types used by moose in that study were often above the 14°C and 20°C thresholds in both day and night. Similarly, we found that ambient temperatures were above the thresholds in northeastern Minnesota. In both Ontario and Minnesota there were periods of 3-5 days in the summer when ambient temperatures remained higher than the thresholds.

In addition to using ambient temperature as a reference, we measured the operative temperature in different cover types. Operative temperature is determined by a black body with the same convection conditions as its environment and produces a net heat flow similar to the heat flow on the surface of an animal (Bakken 1980). Black globe thermometers measure the thermal environment by incorporating ambient temperature, wind

velocity, and radiant energy (Bond and Kelly 1955). Forest canopies filter solar radiation, which causes the greatest difference in equivalent black body temperatures within different cover types (Schwab and Pitt 1991). Increasing crown closure decreases operative temperature as summer thermal cover shelters animals from both heat and radiation. Conifer forests often have high levels of crown closure and have the highest degrees of thermal shelter (Demarchi and Bunnell 1993).

Differences in operative temperature among cover types used by moose were $<2^{\circ}$ C during summer, similar to the small differences in temperature among forest cover types measured in southeastern Ontario (Lowe et

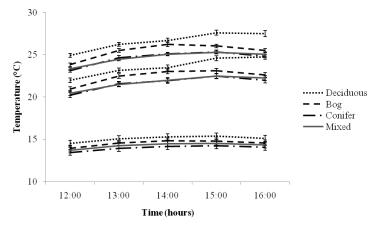


Fig. 3. Average temperatures in cover types in northeast Minnesota during summer afternoons when ambient temperatures exceeded 24.4° C without cloud cover, during hot afternoons, and during afternoons with cloud cover. Vertical error bars represent standard errors.

al. 2010). It seems likely that a 2° C difference among cover types is not biologically significant to moose with regard to selecting cover type. Rather, selective use of cool areas within cover types may be a thermoregulatory strategy of moose. For example, moose bed in water to cool down (Ackerman 1987, Renecker and Hudson 1990). Further, selection and use within cover types for bed sites/microhabitats might relate to the effectiveness of duff layers and soils to act as heat sinks.

It is possible that there are differences in cooling capability in different cover types that could lead to cover type selection. Moose used conifer stands >30 years old and in which conifer represented \geq 75% of the basal area, and also shifted active behavior away from high temperatures of late afternoons (Dussault et al. 2004). Denser canopies of mature forests were used by moose during hot temperatures in British Columbia (Demarchi and Bunnell 1995, Ackerman 1987), and moose in Nova Scotia reduced movement and occupied cooler habitats during hot weather (Broders et al. 2012).

Also, we think it is worth considering the implementation of critical temperature thresholds. Recent papers citing the Renecker and Hudson papers used 14 and 20° C as thresholds, in part because of the explicit identification of increased breathing rates and panting at those temperatures (Renecker and Hudson 1986). However, in a later paper, an upper critical temperature range of 14-20°C is specified (Renecker and Hudson 1990). In addition, Figure 3 of Renecker and Hudson (1986) shows variability in the increase in respiration rate. These differences suggest that Renecker and Hudson did not intend for the 14 and 20°C to be used as predictors of

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	Cover Types			Significance		
Weather Conditions	Deciduous	Bog	Conifer	Mixed	P-value	F3,39
>14°C	$19.2 \pm 0.04 \ a$	$18.4\pm0.04~b$	$18.1\pm0.03~b$	$18.3 \pm 0.03 \ ab$	0.011	4.33
>20°C	$23.8 \pm 0.06 \ a$	$22.7\pm0.05~ab$	$22.0\pm0.04~b$	$22.3\pm0.04~ab$	0.019	3.81
>24.4°C	$26.6 \pm 0.11 \ a$	$25.4\pm0.08~ab$	$24.6\pm0.08~b$	$24.8\pm0.07\;b$	0.012	4.30
Clear days	$15.8 \pm 0.19 \ a$	$14.8\pm0.18~ab$	$15.0\pm0.18~b$	$15.2\pm0.18~b$	< 0.003	5.87
Cloudy days	$12.3 \pm 0.17 \ a$	$12.0 \pm 0.16 \ a$	$11.8 \pm 0.16 \ a$	$12.0 \pm 0.16 \ a$	0.054	2.83
Cloudy afternoons	$15.1 \pm 0.16 a$	$14.5\pm0.16~ab$	$14.0\pm0.15~b$	$14.3 \pm 0.15 \ ab$	0.035	3.23
Clear afternoons	$23.6 \pm 0.44 \ a$	$22.4\pm0.44~ab$	$21.6\pm0.44~b$	$21.7\pm0.44~b$	0.012	4.29
Hot/Clear afternoons	$26.6 \pm 0.13 \ a$	$25.4\pm0.10~ab$	$24.6\pm0.10\;b$	$24.6\pm0.09\;b$	0.012	4.27

Table 1. Temperature differences measured within cover types in northeast Minnesota during summer afternoons under different weather conditions. Letters indicate homogenous groups.

change in habitat use, but rather temperatures at which initial responses might become evident. When we consider the equivocal results of cover type selection, the difference between initiation of a physiological response and implementation of a behavioral response like cover type selection needs to be considered. High temperatures do result in a response by moose, and the ultimate limiting factor for expansion to the south probably remains high temperature (Kelsall and Telfer 1974).

Recent declines in moose populations in Minnesota have been correlated with increasing summer and winter temperatures. The decline in northwest Minnesota was correlated with increases in both summer and winter temperatures (Murray et al. 2006). In contrast, high average January and late spring temperatures explained more of the variability in moose survival in northeast Minnesota (Lenarz et al. 2009, 2010). Summer temperatures are predicted to increase 1.5-2° C by 2025 (Union of Concerned Scientists 2003), and by 3-4° C by 2100 (IPCC 2007). If average summer temperatures continue to increase, then the likely result will be more and longer periods during which temperatures are continuously higher than the upper critical limit for moose.

This study provides information on the potential for available vegetation types in northeast Minnesota to serve as thermal cover. If moose at the southern edge of their range are encountering high temperatures at an increasing and prolonged rate, then their behavior should change. Also, there is a need to measure alternative cooling mechanisms at very fine spatial scale, such as the potential heat sink that cool soils may provide while moose are bedded. Future research should concentrate on how cover types are used when temperatures are high during both summer and winter and how they function to provide thermal relief.

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