FINE-SCALE TEMPERATURE PATTERNS IN THE SOUTHERN BOREAL FOREST: IMPLICATIONS FOR THE COLD-ADAPTED MOOSE

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ABSTRACT: Moose (*Alces alces*) respond to warm temperatures through both physiological and behavioral mechanisms. Moose can reduce heat load via habitat selection when spatial and temporal variation exists within the thermal environment. We recorded operative temperatures (T_o) throughout the Kabetogama Peninsula of Voyageurs National Park, Minnesota for 1 year to describe seasonal patterns in the thermal environment available to moose and identify physical and landscape characteristics that affect T_o in southern boreal forests. Significant predictors of T_o varied by season and time of day and included vegetation cover type, canopy cover, and slope/aspect. Vegetation cover type influenced T_o during summer and fall afternoons with additional variation during summer afternoons explained by percent canopy cover. Slope/aspect was the main driver of T_o during winter and spring afternoons. Slope position was not a significant predictor of temperature, likely because of low topographic relief in our study area. The T_os were significantly warmer in open versus closed habitats during the day with the pattern reversed at night. Our results can be used to test if moose display a behavioral response to T_o at various spatial and temporal scales.

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Key words: *Alces alces*, aspect, canopy cover, cover type, forests, moose, operative temperature, topography.

Moose (*Alces alces)* are adapted to cold environments (Karns 2007) but conversely, are less tolerant of high ambient temperatures (T_a). Renecker and Hudson (1986) estimated the upper critical temperatures (T_{uc}) of moose as −5 °C in winter and 14 °C in summer, with open mouth panting occurring at 0 °C and 20 °C, respectively. A recent study estimated a slightly higher T_{uc} in summer (17 °C; McCann et al. 2013). These estimates of T_{uc} provide a lower limit of T_a at which moose presumably employ physiological and behavioral mechanisms to reduce thermal stress.

Moose respond physiologically to high T_a by reducing metabolic rate, flattening their pelage, and increasing respiratory rate to expel excess heat, but they cannot sweat (Schwartz and Renecker 2007). They also exhibit behavioral responses including higher use of conifer stands for thermal refuge and nocturnal activity (DeMarchi and Bunnel 1995, Dussault et al. 2004, Broders et al. 2012).

Chronic exposure of moose to high T_a has been correlated with reduced weight gain in Norway (van Beest and Milner 2013), lower survival in northeastern Minnesota (Lenarz et al. 2009), population declines in northwestern Minnesota (Murray et al. 2006), and distribution shifts in China (Dou et al. 2013). Fine-scale differences in T_a likely exist across space and time at the southern extent of moose range, and individual moose should exploit these differences to mitigate the effects of high T_a on body

Fig. 1. Cross-section and attached black globe thermometer showing Hobo U22 Water Temp Pro v2 temperature loggers inserted into a 15 cm diameter copper toilet bowl float painted matte black. Loggers were hung 0.75 m above ground and 15 cm from the trunk on the northeast side of a tree.

condition and ultimately fitness. Previous studies of moose habitat selection and T_a focused on forest cover type as the main driver of thermal conditions across the landscape (e.g., Lowe et al. 2010). Other factors affecting variability in the thermal landscape include elevation, canopy cover, slope and aspect, and position on slope (Reifsnyder et al. 1971, Chen and Franklin 1997, Danielson et al. 1997, Chen et al. 1999, Ellis and Pomeroy 2007). Habitat selection patterns relative to T_a cannot be fully understood without a clear understanding of patterns in the thermal environment at different spatial and temporal scales.

Operative temperature (T_o) is an approximation of the convective and radiant heat transfer on the surface of an animal, making it a useful measure to interpret the thermal environment experienced by animals versus T_a alone (Dzialowski 2005). For example, animals experience different T_o in sunlight, wind, or under forest canopy at the same T_a. It is easiest to estimate T_o with a black globe thermometer (Vernon 1930, 1932, 1933; Fig. 1) which consists of a matte black painted copper sphere containing a temperature logger that integrates T_a, mean radiant temperature, and air movements into a single metric (Bedford and Warner 1934).

Our objectives were to identify physical and vegetative factors that influence T_o, and to characterize the thermal environment experienced by moose across different cover types in Voyageurs National Park (VNP) in northeastern Minnesota.

STUDY AREA

Voyageurs National Park (VNP) is situated on the southern limit of North American

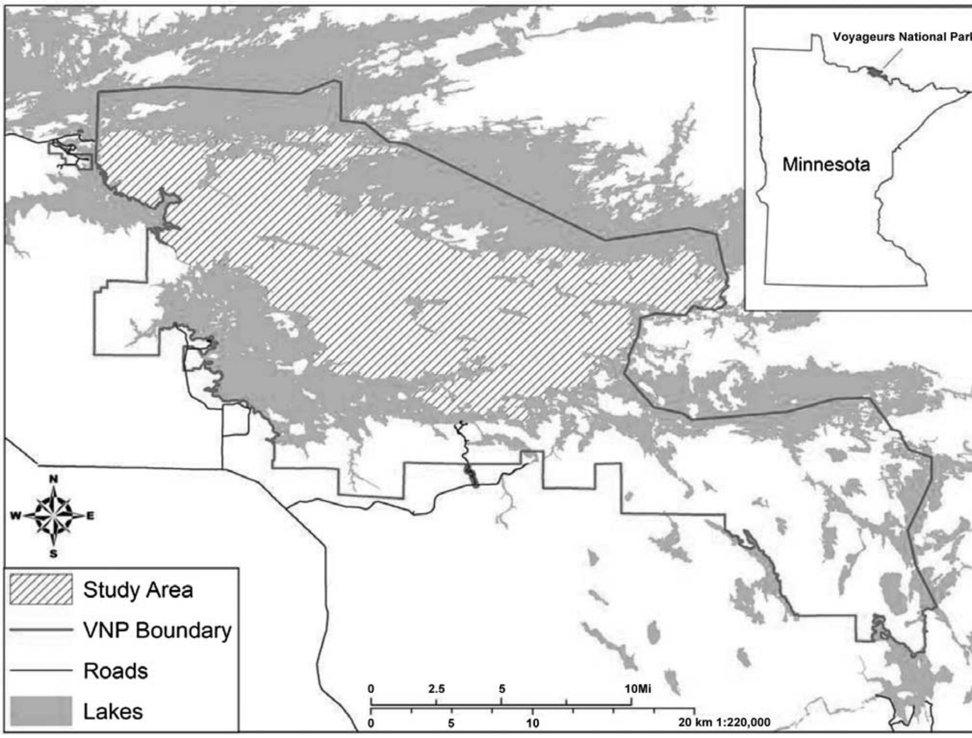

Fig. 2. Location of the Kabetogama Peninsula study area in Voyageurs National Park, Minnesota, USA.

moose range, along the Minnesota-Ontario border (Fig. 2). The climate is mid-continental with long cold winters and short cool summers. Mean monthly temperatures range from −15 °C in January to 19 °C in July with an annual mean temperature of 3 °C (NOAA 2010). First snowfall usually occurs in early November and final snowfall in early April. Average annual precipitation is 61 cm, with an average annual snowfall of 183 cm (NOAA 2010).

We limited the study area to the 329 km^2 Kabetogama Peninsula as this is where most moose in VNP currently reside (Windels 2014, Fig. 2). Vegetation in the Kabetogama Peninsula is typical of the southern boreal and Laurentian mixed conifer-hardwood regions (Faber-Langendoen et al. 2007). Forest cover is a mosaic of quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), and jack (*Pinus banksiana*), red (*P. resinosa*), and white pine (*P. strobus*). A variety of wetlands including bogs, fens, marshes, and swamps are interspersed across the landscape (Faber-Langendoen et al. 2007). Geological features include thin and sandy topsoil with regions of exposed bedrock (Ojakangas and Matsch 1982).

Moose and white-tailed deer (*Odocoileus virginianus*) are the only ungulate species in VNP; woodland caribou (*Rangifer tarandus*) were extirpated by the early 1900s (Cole 1987). Moose density in the Kabetogama Peninsula ranges from 0.14–0.19 moose/km^2 and has remained stable since the 1990s (Windels 2014). Beaver (*Castor canadensis*) are abundant and contribute significantly to the spatial heterogeneity of the landscape (Johnston and Naiman 1990).

A variety of human and other natural disturbances have created a diverse mosaic of vegetation in multiple seral stages. Wildfires and extensive logging occurred in the 1920s and 1930s, followed by less intensive logging through the 1960s (Gogan et al. 1997). Major fires occurred throughout VNP in 1923 and 1936. Suppression of fire followed until the late 1980s when the National Park Service implemented a wildland fire management plan, though most prescribed burns have been relatively small (National Park Service, unpublished data).

METHODS

To measure T_o across the Kabetogama Peninsula, we stratified our sampling design by landscape and vegetation characteristics identified within a 30-m × 30-m pixel matrix that matches with LandSat imagery. We derived slope and aspect for each pixel using 30 m resolution Shuttle Radar Topography Mission data (version 1) (Rabus 2003, Rodriguez et al. 2005, 2006). We estimated slope using the slope function from ERDAS Imagine (ERDAS Inc. 2010). We categorized slope as either <10% (5.7°) or ≥10% (5.7°). We calculated aspect using the aspect function of ERDAS Imagine (ERDAS Inc. 2010) and classified each pixel into 1 of 2 categories: aspects between 315-45° (i.e., north) and aspects between 45-315° (i.e., east/south/west). We assumed that solar inputs would be lower on north facing slopes compared to east, south, and west facing slopes. Therefore, we combined slope and aspect into flat, slopes facing north, and slopes facing east/south/west for analysis. Detectable variation in T_a as a function of elevation was not expected in VNP as most local relief is <30 m and maximum relief within the Peninsula is only 81 m. Therefore, elevation was not considered in our sampling design or subsequent modeling.

We developed a canopy cover model using the methodology outlined in the Great Lakes Inventory and Monitoring Network's Landscape Dynamics protocol (Kennedy and Kirschbaum 2010, Kennedy et al. 2010). Percent cover of trees, shrub, and ground layer was estimated at 30-m pixels in ArcMap (ESRI 2011) using high-resolution air photos taken in the spring (leaf-off) and summer (leaf-on) of 2008 with 0.15 and 1 m resolutions, respectively (Kirschbaum and Gafvert 2010). Estimates of canopy cover in each pixel were related to the normalized burn ratio (van Wagtendonk et al. 2004) calculated from the Landsat image corresponding to that time period to create a regression model of canopy cover. We categorized canopy cover as open (i.e., no or few canopy-forming trees), variable cover (i.e., non-forested, discontinuous canopy), <70% forest cover, 70–80% forest cover, and >80% forest cover. We classified vegetation cover type using the National Vegetation Classification System Subclass Level (deciduous, evergreen, mixed, woodland, shrub, or herbaceous) developed for VNP (Faber-Langendoen et al. 2007).

We developed a sampling matrix using the 3 sets of variables (vegetation cover type, canopy cover, slope/aspect). Each unique combination of the 3 variables was given an identifying code using ERDAS Imagine. A 30-m pixel raster map was created and converted to a polygon shapefile. Areas for each polygon were calculated and polygons <1.07 ha (12 pixels) were deleted to avoid sampling very small patches. We sampled at an intensity of 1 temperature logger for every 333 ha in the study area. We randomly selected polygons to sample from each of 38 unique combinations of vegetation cover type, canopy cover class, and slope/aspect class. We located the sample point near the centroid of the polygon to allow a sufficient buffer between adjacent polygons. We used alternate sites if the selected polygon centroid was <30 m (1 pixel) from the edge, field reconnaissance found that site characteristics were different from remotely-sensed data, or sites were otherwise inaccessible (e.g., flooding).

Black globe temperature loggers consisted of a data-logging thermocouple (Onset Computer Corporation, Bourne, Massachusetts, USA) inserted into a copper toilet tank float painted matte black (Fig. 1). We calibrated loggers for a minimum of 96 h to verify accuracy and resolution as compared to the stated equipment specifications of the logger (±0.21 °C from 0°−50 °C). All loggers were synchronized and programmed to record temperatures every 15 min for 1 year. At each sample point, we hung loggers 0.75 m above the ground and 15 cm from the trunk. Loggers were placed on the northeast side of trees to minimize direct solar radiation during the warmest time of day (Fig. 1). We used handheld field computers with GPS to verify that logger placement in the field was consistent with identified cover type and location within the cover type polygon. We used real-time GIS and measurements in the field to ensure we were within the identified cover type, canopy cover class, and slope/aspect category before deploying loggers. Loggers were deployed from June 2010 to July 2011, with periodic downloads to reduce risk of data loss. Data were screened to remove biased or failed measurements (e.g., faulty logger, damaged globe or logger, and snow-covered loggers).

We deployed an additional set of loggers from August 2011 to January 2012 to test for differences in position on slope. We randomly deployed 3 loggers in each of 9 combinations of cover type (deciduous, evergreen, and mixed), canopy cover class (<70%, 70–80%, >80% forested canopy), and slope position (top, mid-slope, and base); slopes ranged from 17–47%.

We analyzed data by season with full factorial repeated-measures ANOVA with type III sums of squares using SPSS 20 (IBM Corporation 2011). We defined seasons as spring (1 March–31 May), summer (1 June–31 August), fall (1 September–30 November), and winter (1 December–28 February). Each 15 min logger interval was treated as the response variable but controlled for repeated measures. Post-hoc pairwise comparisons were made using the Bonferroni method. Significance levels were set to P = 0.05 for all tests. Subsamples of the dataset were made to compare differences during the 3 warmest hours of the day (1300–1600 hr) and the 3 coldest hours of the day (0300–0600 hr). We used a similar statistical approach to test for differences in slope position for summer and winter only.

Based on model results, we assessed the availability of potential thermal refugia to moose across the Kabetogama Peninsula. We simulated moose home ranges by creating 25 random points within the study area and then buffering those points to approximate mean annual moose home ranges in VNP (48 km^2 ± 33.5 SD) as reported by Cobb et al. (2004). Home ranges varied in size due to the highly variable shoreline of the Kabetogama Peninsula. Within each simulated home range, we estimated the proportion of each habitat type (vegetation cover type, canopy cover class, slope/aspect) and used summary statistics to highlight availability of selected habitat features.

RESULTS

Open habitat types (shrub and herbaceous) were significantly warmer than forested habitat types during the summer (maximum difference = 3.38 °C; Fig. 3) with the greatest difference occurring in the afternoon (maximum difference = 8.10 °C; Table 1, Fig. 3). Open habitat types were also the coolest at night (maximum difference = 2.66 °C; Table 1, Fig. 3). Mean T_o during the summer did not differ among forested cover types for any of the time periods (Daily, Hot, Cold). Herbaceous cover types were warmer than forested cover types in the afternoon during the fall (maximum

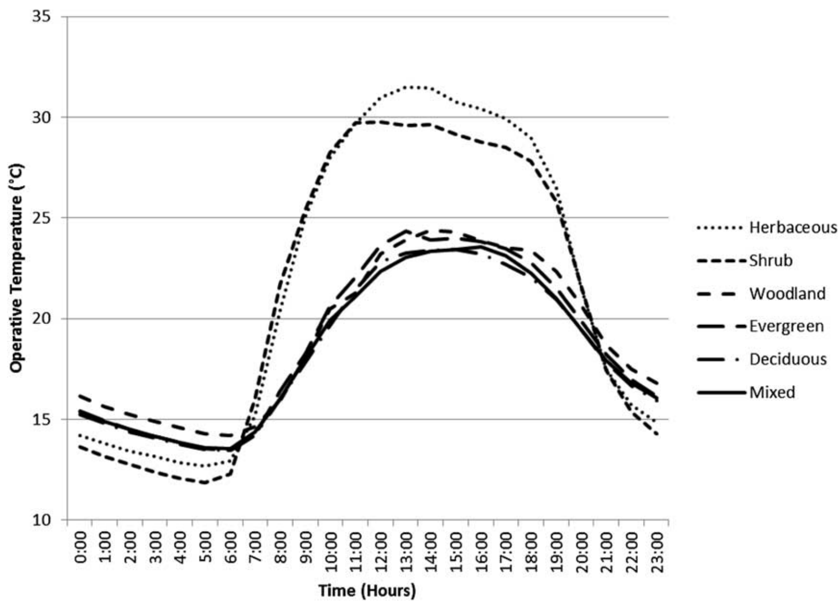

Fig. 3. Mean operative temperatures across vegetation cover types in summer over a 24-hour period, 1 June–31 August 2010, Voyageurs National Park, Minnesota, USA.

difference = 7.43 °C; Table 1, Fig. 3). Temperatures in shrub cover types were intermediate between herbaceous and forested cover types. The amount of canopy influenced T_o within forested cover types. Areas with >80% canopy coverage were cooler than those with <70% cover (Table 2, Fig. 4); T_o in the 70–80% cover class was intermediate to these.

Slope/aspect influenced T_o only during the 3 coldest hours of day in summer. Flat areas were cooler than East/South/West facing slopes (difference = 1.14 °C; Table 3). North-facing slopes were intermediate between flat areas and East/South/West facing slopes. Slope/aspect had no influence on T_o during the fall months. Winter temperature was only differentiated by slope/aspect during the afternoon with northern facing slopes cooler than both flat and east/south/west categories (Table 3, Fig. 5). Spring temperatures varied across slope/aspect categories during the afternoon hours. North-facing slopes were cooler than flat areas (Table 3, Fig. 5). T_o was not different among slope positions in summer ($F_{2,21}$ = 0.287, P = 0.755) or winter ($F_{2,21}$ = 0.606, P = 0.556).

The majority of the Kabetogama Peninsula consists of forested cover types with >70 percent canopy cover and flat topography (Table 4, Fig. 6, 7). Simulated home ranges varied in size from 23–57 km^2 with a mean of 46 km^2 (SD = 10.1 km^2). Potential summer refugia, such as high-canopy cover forests, were found in about 40% of simulated home ranges (Table 4). However, north-facing slopes are relatively limited in the study area and the percentage of north-facing slopes in simulated home ranges was <10% (Table 4, Fig. 7).

DISCUSSION

Vegetation cover type, percent canopy cover, and slope/aspect all influenced T_o, although differently depending on season and time of day. Vegetation cover type had the strongest influence on T_o during summer months and fall afternoons. This was largely

Table 1. Mean daily (24-hour mean) operative temperatures (°C) across vegetation cover types in spring (1 March–31 May 2011), summer (1 June–31 August 2010), fall (1 September–30 November 2010), and winter (1 December 2010–28 February 2011), Voyageurs National Park, Minnesota, USA. Mean operative temperature for the 3 warmest (Hot) and 3 coldest (Cold) hours of the day are also shown. Means followed by the same letter within a row are not significantly different from each other.

		Vegetation Cover Type												Significance	
Season		Deciduous		Evergreen		Mixed		Woodland		Shrub		Herbaceous		$F_{5,85}$	*P* Value
Sprint	Daily	3.97 ± 0.74	*ab*	2.89 ± 0.78	*a*	4.28 ± 0.73	*ab*	3.53 ± 1.81	*ab*	5.26 ± 1.48	*ab*	6.70 ± 1.15	*b*	0.86	0.496
	Hot	10.47 ± 0.90	*a*	7.95 ± 0.95	*b*	10.29 ± 0.90	*ab*	9.23 ± 2.21	*abc*	14.19 ± 1.80	*ac*	16.63 ± 1.40	*c*	2.59	0.051
	Cold	−1.45 ± 0.65	*a*	−1.71 ± 0.68	*a*	−1.25 ± 0.64	*a*	−1.71 ± 1.59	*a*	−1.64 ± 1.01	*a*	−2.39 ± 1.30	*a*	0.14	0.934
Summer	Daily	18.32 ± 0.33	*a*	18.76 ± 0.35	*a*	18.42 ± 0.33	*a*	19.33 ± 0.60	*ab*	21.25 ± 0.60	*bc*	21.70 ± 0.42	*c*	2.93	0.029
	Hot	23.03 ± 0.57	*a*	23.66 ± 0.60	*a*	23.13 ± 0.57	*a*	24.52 ± 1.04	*a*	29.84 ± 1.04	*b*	31.13 ± 0.73	*b*	7.10	<0.001
	Cold	13.76 ± 0.37	*a*	13.97 ± 0.39	*ab*	13.54 ± 0.37	*ab*	14.68 ± 0.67	*b*	12.88 ± 0.47	*ab*	12.02 ± 0.67	*a*	2.86	0.045
Fall	Daily	5.56 ± 0.65	*a*	5.56 ± 0.69	*a*	5.66 ± 0.67	*a*	5.99 ± 1.18	*a*	6.38 ± 1.18	*a*	7.49 ± 0.83	*a*	0.32	0.862
	Hot	9.97 ± 0.82	*ab*	9.26 ± 0.87	*ab*	9.77 ± 0.85	*ab*	10.48 ± 1.49	*ab*	14.24 ± 1.49	*ac*	16.69 ± 1.05	*c*	3.00	0.026
	Cold	2.48 ± 0.57	*a*	2.78 ± 0.60	*a*	2.63 ± 0.59	*a*	2.93 ± 1.03	*a*	2.23 ± 0.73	*a*	1.52 ± 1.03	*a*	0.35	0.786
Winter	Daily	−13.37 ± 0.24	*a*	−12.99 ± 0.25	*a*	−13.41 ± 0.25	*a*	−13.25 ± 0.44	*a*	−14.58 ± 0.44	*a*	−14.20 ± 0.36	*a*	1.70	0.166
	Hot	−9.20 ± 0.40	*ab*	−9.68 ± 0.43	*a*	−9.72 ± 0.42	*a*	−9.15 ± 0.73	*ab*	−9.08 ± 0.73	*ab*	−6.95 ± 0.60	*b*	2.14	0.091
	Cold	−16.17 ± 0.33	*a*	−15.59 ± 0.35	*a*	−16.02 ± 0.34	*a*	−16.10 ± 0.60	*a*	−17.22 ± 0.49	*a*	−17.30 ± 0.60	*a*	1.19	0.324

Table 2. Mean daily (24-hour mean) operative temperatures (°C) across varying amounts of canopy cover by season in spring (1 March–31 May 2011), summer (1 June–31 August 2010), fall (1 September–30 November 2010), and winter (1 December 2010–28 February 2011), Voyageurs National Park, Minnesota, USA. Mean operative temperature for the 3 warmest (Hot) and 3 coldest (Cold) hours of the day are also shown. Means followed by the same letter within a row are not significantly different from each other.

		Canopy Cover										Significance	
Season		Open		Variable		<70%		70–80%		>80%		$F_{4,85}$	*P* Value
Spring	Daily	6.70 ± 1.15	*a*	4.40 ± 1.17	*a*	4.47 ± 0.75	*a*	3.14 ± 0.77	*a*	3.47 ± 0.72	*a*	0.59	0.561
	Hot	16.46 ± 1.35	*a*	11.67 ± 1.38	*a*	10.99 ± 0.92	*ab*	8.66 ± 0.94	*bc*	9.00 ± 0.88	*bc*	1.38	0.265
	Cold	−1.644 ± 1.01	*a*	−2.05 ± 1.03	*a*	−1.27 ± 0.66	*a*	−1.87 ± 0.68	*a*	−1.31 ± 0.64	*a*	0.25	0.783
Summer	Daily	21.70 ± 0.42	*a*	20.29 ± 0.42	*a*	19.00 ± 0.35	*b*	18.54 ± 0.34	*bc*	17.96 ± 0.31	*c*	2.48	0.093
	Hot	30.93 ± 067	*a*	27.09 ± 0.67	*b*	24.39 ± 0.61	*c*	23.24 ± 0.59	*cd*	22.18 ± 0.54	*d*	3.71	0.031
	Cold	12.88 ± 0.47	*a*	13.35 ± 0.47	*a*	13.49 ± 0.39	*a*	13.95 ± 0.38	*a*	13.83 ± 0.35	*a*	0.38	0.688
Fall	Daily	7.48 ± 0.83	*a*	6.18 ± 0.83	*a*	5.57 ± 0.69	*a*	5.73 ± 0.67	*a*	5.48 ± 0.65	*a*	0.04	0.965
	Hot	16.39 ± 1.01	*a*	12.36 ± 1.01	*a*	10.25 ± 0.88	*b*	9.79 ± 0.85	*b*	8.95 ± 0.81	*b*	0.62	0.541
	Cold	2.23 ± 0.73	*a*	2.23 ± 0.73	*a*	2.40 ± 0.61	*a*	2.69 ± 059	*a*	2.81 ± 0.56	*a*	0.13	0.879
Winter	Daily	−14.20 ± 0.36	*a*	−13.92 ± 0.31	*a*	−13.45 ± 0.26	*a*	−13.28 ± 0.25	*a*	−13.07 ± 0.24	*a*	0.57	0.569
	Hot	−7.11 ± 0.53	*a*	−8.82 ± 0.46	*a*	−8.94 ± 0.43	*a*	−9.70 ± 0.42	*b*	−10.02 ± 0.40	*b*	1.75	0.184
	Cold	−17.22 ± 0.49	*a*	−16.70 ± 0.42	*a*	−16.29 ± 0.35	*a*	−15.98 ± 0.34	*a*	−15.50 ± 0.33	*a*	1.39	0.259

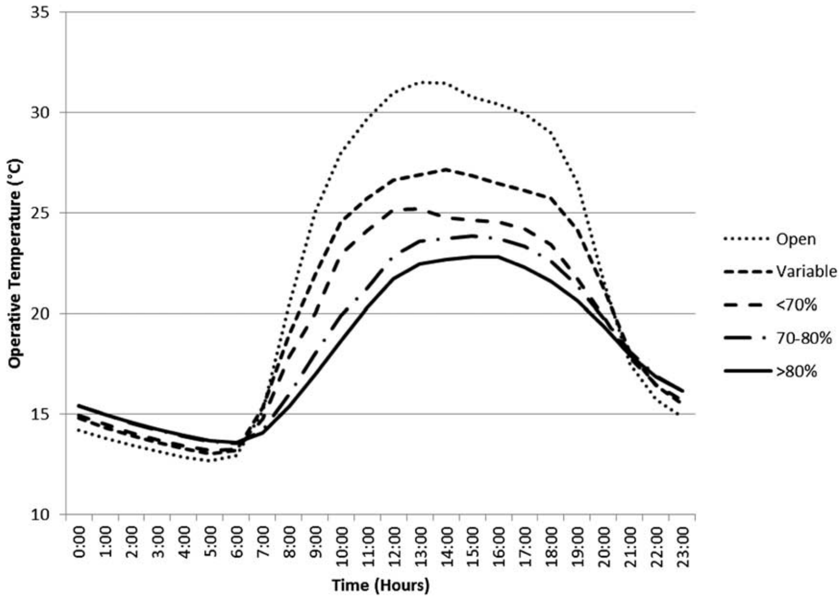

Fig. 4. Mean operative temperatures across varying amounts of canopy cover in summer over a 24-hour period, 1 June–31 August 2010, Voyageurs National Park, Minnesota, USA.

Table 3. Mean daily (24-hour mean) operative temperatures (°C) across slope/aspect categories in spring (1 March–31 May 2011), summer (1 June–31 August 2010), fall (1 September–30 November 2010), and winter (1 December 2010–28 February 2011), Voyageurs National Park, Minnesota, USA. Mean operative temperature for the 3 warmest (Hot) and 3 coldest (Cold) hours of the day are also shown. Means followed by the same letter within a row are not significantly different from each other.

		Slope / Aspect						Significance	
Season		Flat		East/South/West		North		$F_{2,85}$	*P* Value
Spring	Daily	4.15 ± 0.39	*a*	4.48 ± 0.88	*a*	2.87 ± 0.91	*a*	0.61	0.551
	Hot	11.14 ± 0.48	*a*	11.05 ± 1.07	*ab*	7.27 ± 1.10	*b*	3.36	0.045
	Cold	−1.79 ± 0.35	*a*	−1.07 ± 077	*a*	−1.57 ± 0.80	*a*	0.20	0.816
Summer	Daily	18.79 ± 0.16	*a*	19.01 ± 0.37	*a*	18.35 ± 0.40	*a*	2.16	0.125
	Hot	24.73 ± 0.28	*a*	24.03 ± 0.65	*ab*	22.30 ± 0.69	*b*	1.76	0.181
	Cold	13.03 ± 0.18	*a*	14.17 ± 0.42	*b*	14.11 ± 0.45	*ab*	4.92	0.011
Fall	Daily	5.32 ± 0.33	*a*	6.34 ± 0.76	*a*	5.56 ± 0.79	*a*	1.54	0.225
	Hot	10.60 ± 0.41	*a*	10.92 ± 0.96	*a*	8.55 ± 0.99	*a*	1.50	0.233
	Cold	1.86 ± 0.29	*a*	3.08 ± 0.67	*b*	3.07 ± 0.69	*ab*	2.60	0.084
Winter	Daily	−13.41 ± 0.12	*a*	−12.84 ± 0.28	*a*	−13.74 ± 0.29	*a*	2.45	0.097
	Hot	−8.89 ± 0.21	*a*	−8.35 ± 0.47	*a*	−11.22 ± 0.49	*b*	10.24	<0.001
	Cold	−16.18 ± 0.17	*a*	−15.84 ± 0.39	*a*	−15.99 ± 0.40	*a*	0.041	0.959

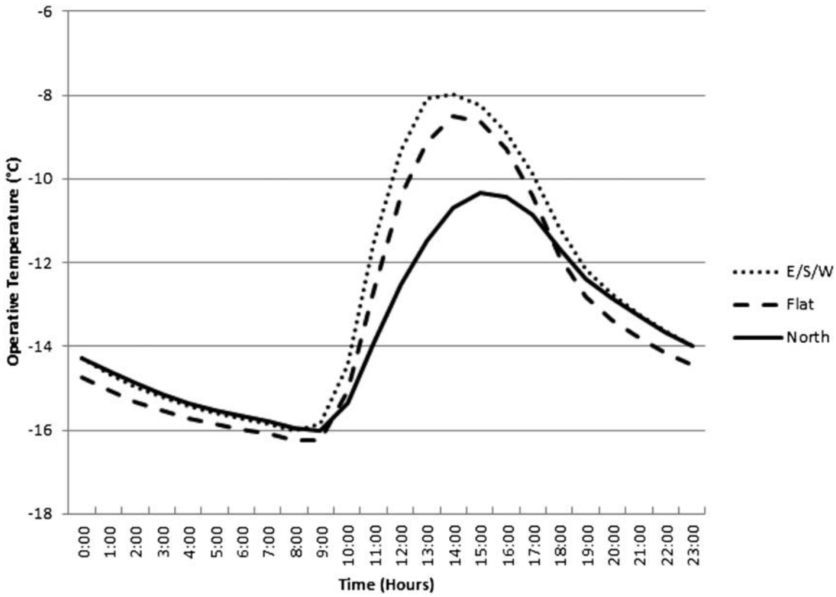

Fig. 5. Mean operative temperatures across slope/aspect categories in winter over a 24-hour period, 1 December 2010–28 February 2011, Voyageurs National Park, Minnesota, USA.

Table 4. Mean, standard deviation (SD), minimum (Min), and maximum (Max) percentage of vegetation cover type, canopy cover, and slope/aspect categories in 25 simulated moose home ranges in Voyageurs National Park, Minnesota, USA.

		Simulated Home Range			
Variable		Mean	SD	Min	Max
Vegetation Cover Type	Evergreen	13	5	6	23
	Deciduous	34	11	20	58
	Mixed	27	7	14	48
	Woodland	4	2	1	7
	Shrub	6	4	2	16
	Herbaceous	16	8	8	36
Canopy Cover Class	High	41	6	29	52
	Med	23	6	13	34
	Low	10	4	4	15
	Variable	10	3	5	16
	Open	16	8	8	36
Slope / Aspect	East/South/West	8	4	2	13
	Flat	87	5	79	96
	North	5	2	2	8

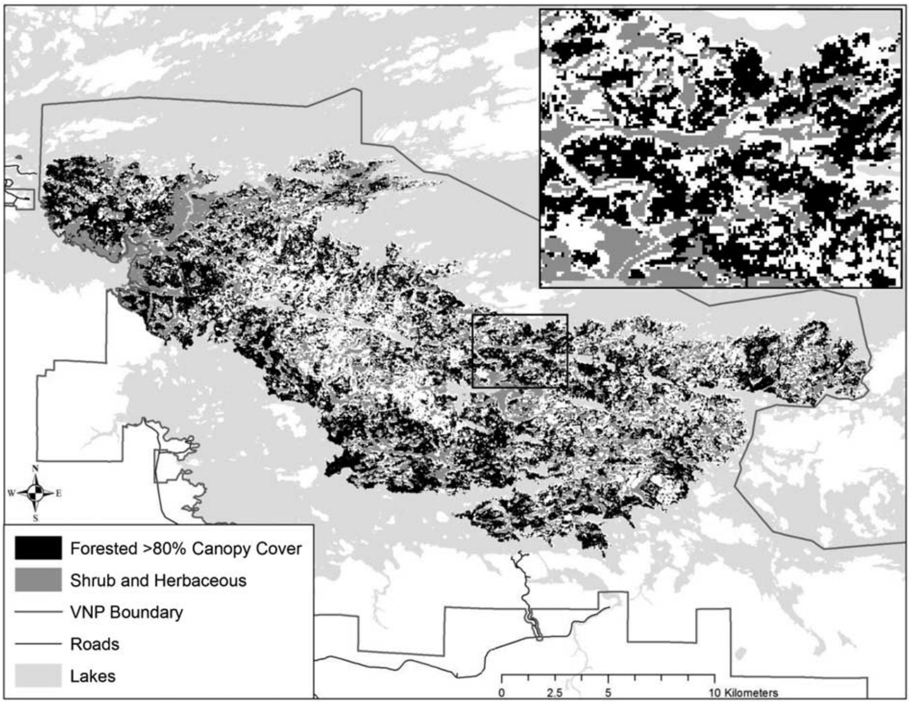

Fig. 6. Spatial distribution of potential summer thermal refugia across the Kabetogama Peninsula in Voyageurs National Park, Minnesota, USA. Forested areas with >80% canopy cover are coolest during the day (black pixels) while herbaceous and shrub cover types (gray pixels) are coolest at night. All other habitat types are shown as white. Inset shows fine-scale juxtaposition of "cool" and "hot" habitats at 30-m pixel resolution.

driven by open versus forested habitats, although we detected small but significant differences in T_o within closed forest habitats, similar to other studies (e.g., McGraw et al. 2012). Amount of canopy cover significantly affected T_o only during afternoons in the summer months. Forest type and the amount of canopy cover effectively combine to reduce the amount of solar radiation that reaches the forest floor and therefore can reduce heat loading from direct solar radiation (Demarchi and Bunnel 1993). Vegetation volume, hence canopy cover, is greatest in summer months, likewise solar angle is most direct during summer afternoons. Areas with thick vegetation and dense canopy cover may serve as ideal thermal refuge for moose during the day (DeMarchi and Bunnell 1995, Dussault et al. 2004, van Beest et al. 2012). Although some variation exists in the amount of forested habitat types with high canopy cover within our simulated home ranges, these habitat types do not seem limited in the study area.

Open cover types were cooler than forested cover types during the 3 coldest hours of the day. Dense vegetation and canopy cover actually retain heat within forested cover types while open cover types release more heat at night (Chen et al. 1993). Moose in central Norway use open habitat types at night and older forested stands during daytime (Bjørneraas et al.

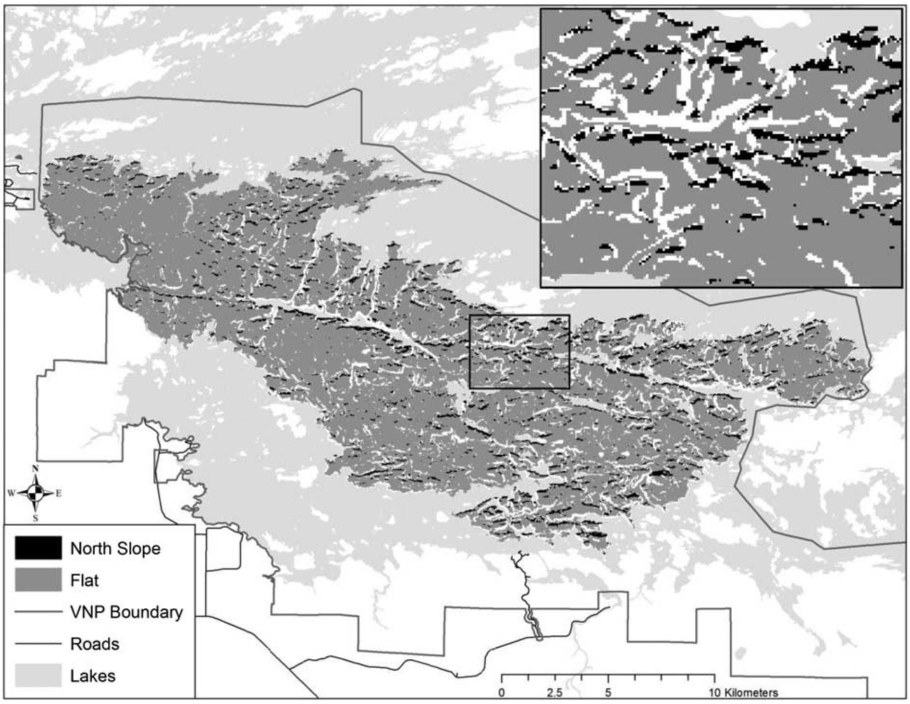

Fig. 7. Spatial distribution of potential winter and spring thermal refugia (i.e., north-facing slopes; black pixels) across the Kabetogama Peninsula in Voyageurs National Park, Minnesota, USA. Areas with flat aspect are shown for comparison (gray pixels). All other habitat types are white. Inset shows fine-scale juxtaposition of north-facing slopes with other aspects at 30-m pixel resolution.

2011). The availability of open cover types may be limited for some moose in the Kabetogama Peninsula.

We defined 4 equal seasons in our models based on calendar months rather than the timing of leaf phenology which varies annually in response to weather events, disease, drought, and other factors (Lechowicz 1984). As a consequence, our ability to detect significant differences may have been diminished for some variables, specifically canopy cover. Future studies of T_o should consider incorporating important predictor variables that may change at relatively fine time scales. Also, canopy cover estimates were based on the leaf-on period, and may not accurately reflect the true amount of canopy cover during leaf-off periods for all cover types with a deciduous tree component.

The majority of the study area was flat and cooler at night than east/south/west facing slopes during summer, likely due to differences in radiant heat loss. Slope/aspect was the only significant influence on T_o during winter months as well as spring afternoons. Slope/aspect may have a stronger effect on T_o during winter months when the solar angle is at its lowest. These environments may serve as thermal refugia on warm days in winter and early spring as topographic exposure can influence maximum daily temperatures (Bolstad et al. 1998). Additionally, radiation received on flat and south facing slopes may be reflected to the body by the high reflectivity of snow in winter. More northerly locations may realize increased effect of slope/aspect, as well as areas with greater topographic relief. Moose strongly selected north-facing slopes in southwestern Alberta due to increased shade and browse availability (Telfer 1988). North-facing slopes make up less than 5 percent of our study area and across most simulated home ranges, suggesting this type of seasonal thermal refugia may be limited for moose in our study area.

We did not detect an effect of slope position on T_o, presumably because of the low topographic relief in the study area (Danielson et al. 1997). Areas with larger elevational gradients than our study area should include elevation as a variable due to the adiabatic lapse or rate change in temperature of an air mass as it changes with altitude (American Meteorological Society 2000). In certain studies elevation was the single strongest driver of temperature difference (e.g., Lookingbill and Urban 2003).

Moose use aquatic habitats for a variety of reasons including foraging, sodium acquisition, insect relief, and thermoregulation (Peek 2007). Aquatic habitats in our study area contain little to no canopy cover and related T_o regimes are likely similar to that of open habitat types. Although moose using shallow, aquatic habitats during daytime may be exposed to direct solar radiation, they could mitigate heat loading by submerging in water.

Thermal variability exists at relatively fine scales across our study area due primarily to the fine mosaic of vegetation cover types, canopy coverage, and site aspect (Fig. 6, 7). We detected maximum differences in mean T_o of ≤ 9 °C across all habitat types during the warmest parts of summer days. Within forested habitat types, there was >2 °C difference across canopy cover categories in summer. Slope/aspect accounted for as much as a 4 °C difference in T_o during winter and spring. Even small differences in the thermal environment may be relevant for achieving individual heat balance (Renecker and Hudson 1990).

The availability of thermal refugia will be of greater importance at the southern edge of moose range as mean annual temperature continues to rise with climate change (IPCC 2007). Behavioral responses to high T_a include specific microhabitat use and activity shifts in other parts of moose range (Dussault et al. 2004, Broders et al. 2012, van Beest et al. 2012). To mitigate the effects of increasing T_a, managers should promote a variety of habitat types to provide adequate thermal refugia within a typical home range while meeting other life history requirements of moose (Peek 2007).

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