RELATING AMBIENT AND BODY TEMPERATURE IN FREE-RANGING MOOSE: IMPLICATIONS TO HEAT STRESS AND SURVIVAL IN MINNESOTA

Michelle Carstensen[1], Véronique St-Louis[2], and Andrew Tri[3]

[1]Wildlife Health Program, Minnesota Department of Natural Resources, Forest Lake, Minnesota, 55025, USA; [2]Wildlife Biometrics Unit, Minnesota Department of Natural Resources, Forest Lake, Minnesota, 55025, USA; [3]Forest Populations and Research Group, Minnesota Department of Natural Resources, Grand Rapids, Minnesota, 55744, USA.

ABSTRACT: Climate change, or more explicitly heat stress, has been implicated as a driver of the rapid decline to Minnesota's moose (*Alces alces*) population over the past 20 years. While often inferred that moose become heat stressed when ambient temperature exceeds thermal thresholds derived from captive moose, few studies provide physiological data to support that wild moose experience heat stress. Our study goals were to measure and explore relationships between ambient temperature and body temperature (T_b) of moose and evaluate their potential influence on heat stress and survival. We obtained continuous measurements of internal T_b of wild moose (n = 41; 23 females, 18 males) from 2013–2017 with mortality implant transmitters (MIT). We examined how frequently moose experienced ambient temperatures above reported upper critical temperatures (thresholds) in winter and summer that cause increased metabolism and panting. Moose often experienced days when ambient temperature was above all thresholds during summer (49.3–92.5% of summer days) and winter (36.3–78.5% of winter days). The percentage of days when a moose exhibited above normal T_b (≥ 39.17 °C) varied significantly between seasons, with conditions most likely to exceed the thresholds during summer (44–51% of summer days) but not winter**.** We found maximum daily T_b increased significantly with increasing maximum daily ambient temperature in summer. Predictions from our models suggest that moose in summer may experience elevated T_b, potentially indicative of heat stress, at maximum daily temperatures > 25 °C. We found T_b was most often higher in the evenings and overnight, as 76% of hot T_b occurred between 18:00–6:00 hr. The duration a moose maintained an elevated internal T_b was highly variable (mean = 32 min, range = 5 to 1,065 min). We also found that moose survival was related to the number of hot moose events (HME) they experienced on an annual basis. Moose that died (n = 14) had 2.0–2.8 x higher average HME per day than survivors over the course of a year. Our findings highlight the need for physiological data to support behavioral observations related to how endotherms respond to ambient temperature changes. Presumably, moose adopt behavioral tradeoffs in summer to mitigate heat stress that may reduce overall fitness and survival.

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Moose (*Alces alces*) are an iconic, cold-adapted species associated with boreal forest habitats, and considered threatened by climate change across their range in North America and worldwide (Karns 2007, Dou et al. 2013, Monteith et al. 2015, Weiskopf et al. 2019). Population decline in portions of their southern historic range (Jensen et al. 2018) is associated with numerous climate and non-climate related factors including predation, parasites, forest management, hunting, and habitat loss (Murray et al. 2006, 2012, Mech and Fieberg 2014, Hasbrouck et al. 2020, Wittische et al. 2021, Marrotte et al. 2022, Peterson et al. 2022). Moose in northwestern Minnesota are nearly extirpated, and the northeast population has declined by 60% since 2006 (Giudice 2023). Climate change and more explicitly, heat stress, has been implicated (through correlation) as a primary cause of the Minnesota moose decline (Murray et al. 2006, Lenarz et al. 2009, 2010). This inference is based upon comparing increasing regional ambient temperatures to the upper critical temperature thresholds measured in 2 captive moose (Renecker and Hudson 1986); however, direct extrapolation of these measurements as an operative temperature, thermal stress, or survival threshold of free-ranging moose is overly simplistic. These studies lack any physiological or empirical data to support that heat stress occurs at a level sufficient to evoke an individual mortality response or population decline.

Heat stress is a medical term that describes a physiological condition in which both body temperature (T_b) and heart rate increase beyond the normal range for a species, leading to acute changes in energy balance and metabolism and, if chronic, increased incidence of disease and poor health (Wills 2016, Collier et al. 2017). At normal T_b of 38.4–38.9 °C (Franzmann et al. 1984), moose employ behavioral thermoregulation by using cover and microhabitats to mediate radiant temperature and access/avoid wind and precipitation, and shift activity and energy budgets (McGraw et al. 2012, McCann et al. 2016, Street et al. 2016). Although limited in animal sample size and fasted animals, two studies provide upper critical temperature thresholds of moose. Renecker and Hudson (1986) found increased metabolism and panting in moose at -5.1 and -2.2 °C in winter and 14 and 20 °C in summer. McCann et al. (2013) later measured a summer threshold of 17 °C without wind and 24 °C in constant 11.3 mph wind from observations of panting. Again, extrapolating critical temperature thresholds to free-ranging moose across northern latitudes where animals commonly seek thermal refugia in diverse microhabitats is questionable (Lowe et al. 2010, Olson et al. 2014, Street et al. 2015). Recently, Thompson et al. (2020*a*) measured T_b of semi-captive moose in Alaska to test the critical threshold of 14 °C in summer and found no evidence of a heat stress response. Rather, T_b was most influenced by the interaction of ambient temperature and vapor pressure, and daily weather patterns influenced physiological and behavioral responses to dissipate heat. Further, Thompson et al. (2019) found a daily rhythm in summer T_b that ranged 0.9 °C; T_b was concentrated from 37–39 °C year-round.

Recent advancements in biotechnology allow repeated measure of T_b in ruminants, including moose (Signer et al. 2010, Herberg et al. 2018, Thompson et al. 2019, Græsli et al. 2020 *a, b*). Here, we are the first to deploy a rumen bolus, or mortality implant transmitter (MIT), to a large number of free-ranging moose in North America. The bolus was designed originally to detect heart activity and provide instantaneous notification of death through the animal's paired radio-collar; however, it is also capable of recording T_b. Herberg et al. (2018) determined the device to be highly accurate at estimating core T_b, providing the opportunity to evaluate how wild moose respond to warm environmental conditions.

Our goal was to explore the relationship between ambient temperature and T_b of moose with 4 specific objectives: 1) determine if T_b of moose is related to ambient temperature, 2) determine if wild moose have elevated T_b when exposed to ambient temperatures above critical temperature thresholds reported in captive moose, 3) determine if moose experience above normal T_b and if so, describe the timing and duration of these events, and 4) assess if survival is impacted by heat stress.

METHODS

Study Area and Moose Capture

In 2013–2015, we captured moose (>1 year-old, n = 173) within a 3,733 km^2 study area located between 47° 12'N and 47° 95'N latitude and 90° 33'W and 91° 72'W longitude in northeastern Minnesota (Fig. 1) as part of a survival and cause-specific mortality study (see Carstensen et al. 2014, 2017). This region has been classified as Northern Superior Upland (Minnesota Department of Natural Resources [MNDNR] 2015) and includes bogs, swamps, lakes, and streams with lowland stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*), and upland stands of balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), white pine (*P. strobus*), and red pine (*P. resinosa*); trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and conifers are intermixed. White-tailed deer (*Odocoileus virginianus*) occur throughout the study area, with wolves (*Canis lupus*) and American black bears (*Ursus americanus*) the primary predators of moose and deer (Fritts and Mech 1981, Nelson and Mech 1986).

All moose were fitted with GPS-Iridium satellite collars (Vectronic Aerospace GmbH; Berlin, Germany) to monitor daily survival and record locations at ~ 4-h intervals. The

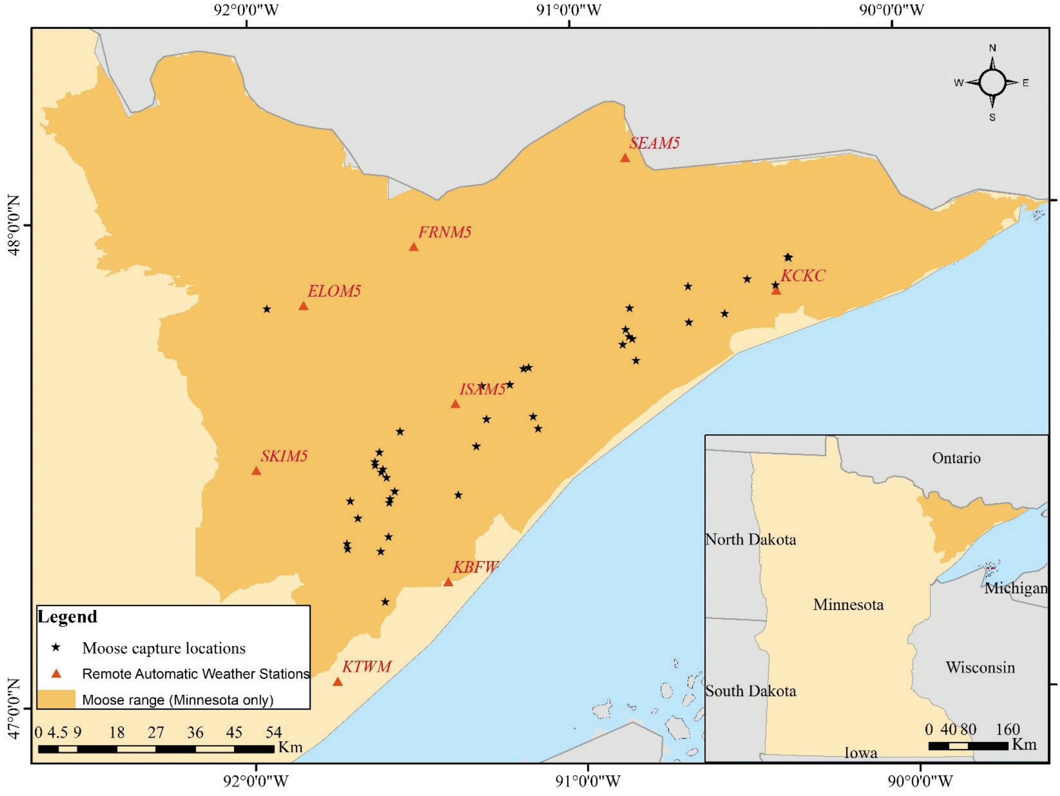

Fig. 1. Capture locations of 41 free-ranging moose implanted with internal temperature loggers from 2013–2017, in northeast Minnesota, and the spatial distribution of 8 Remote Automatic Weather Stations.

MITs (Vectronic Aerospace GmbH) were placed orally into the reticulum of 41 animals (22 females, 19 males) in 2013 (n = 11 moose), 2014 (n = 13), and 2015 (n = 17) and were programmed to record T_b (0.1 °C accuracy, Vectronic Aeorspace GmbH) at either 10- or 15-min intervals (Herberg et al. 2018, Minicucci et al. 2018). Age was determined by cementum annuli analysis (Matson's Lab, Manhattan, Montana) of a lower incisiform canine tooth removed at capture (40 of 41 moose). Age varied from 1 to 16 years old (median = 6 years) within three age classes: young (≤ 3 years, n = 10), prime (4–8 years, n = 20), and old (≥ 9 years, n = 10). All MIT readings obtained 1 week post-capture and 1 week pre-death were excluded from analyses to reduce potential effects of capture stress and mortality on moose T_b (Thompson et al. 2020b). Moose were censored on the date their collar stopped transmitting data, regardless of their survival state.

Weather Data and Seasons

Minnesota has a humid continental climate, characterized by hot summers and cold winters. Ambient temperature is as low as -51 °C in winter and as high as 45 °C in summer (MNDNR 2024), with daily maximum temperatures in summer typically 20 to 30 °C (see RESULTS). The moderating effect of Lake Superior keeps the northeast region relatively cooler in summer and warmer in winter compared to most of the state. The MNDNR assesses winter severity (1 November–31 May) with a Winter Severity Index (WSI) calculated by accumulating a daily score of 0–2 points: 1 point when daily temperature is ≤ −17.7 °C and 1 point when daily snow depth is ≥38 cm. Maximum WSI values in moose range across 6 winters (2012–13 to 2017–18) varied markedly, ranging from 35–160, 184–245, 54–152, 31–142, 50−159, and 50−179, respectively (MNDNR 2024). We used data from 8 weather stations located in Ely (ELOM5), Fernberg (FRNM5), Grand Marais (KCKC), Isabella (ISAM5), Seagull (SEAM5), Silver Bay (FBFW), Skibo (SKIM5), and Two Harbors (KTWM) (Fig. 1) that were part of the network of Forest Service Remote Automated Weather Stations (RAWS) (Zachariassen et al. 2003) within the study area. All stations operated for the entire study period except SKIM5 which became operable in April 2015.

We summarized ambient temperature (measured 2 m above ground), precipitation, and wind speed that each moose potentially experienced at a given point in time by utilizing the 4-h location data. We first generated time series that included the exact times of MIT readings (10- or 15-min resolution) for each animal and merged with the time series of the location data (1- or 4-h intervals). We approximated the location of moose at the time of the MIT readings by linearly interpolating the geographic locations (converted from lat-long to UTMs NAD83 Zone 15) between each 1- or 4-h interval. We acknowledge that moose do not move in a linearly fashion between time steps; however, this represents an approximation of the general location where a moose was at a given point in time. We assigned the nearest RAWS to each approximate location (at times of MIT recordings) by calculating the minimum Euclidean distance between a moose location and the 8 RAWS available within the study area. We then merged the weather station data to the nearest RAWS time series and used this as our best estimate of the weather conditions a given moose experienced at a given point in space and time. As moose move, the closest weather station may change and thus it was possible to have data from different weather stations for a given moose. The average distance between moose locations and the nearest weather station at any given point in time varied between 5 and 36 km for 40 of the moose. We recognize that microhabitats occupied by moose would not necessarily expose moose to wind speed or precipitation measured at the weather stations; however, ambient temperature should be reasonably similar.

Four seasons were set annually by averaging ambient temperature and snow depth data across the 8 RAWS as follows: fall began at the date of first frost with temperatures < 0 °C; winter began with snow depth consistently > 4 inches (10.16 cm); spring began when snow depth was consistently < 4 inches and included parturition; summer began as spring/parturition ended (Table 1). Parturition for females include 21 days pre- and post- of the mean parturition date reported by Severud et al. (2015).

Identifying Heat Days and Hot Moose Events

We categorized each ambient temperature value as being equal or above (Heat Threshold [HT] = 1) or below (HT = 0) the Renecker and Hudson (1986) thresholds of -2.2 and -5.1 °C in winter and 20 and 14°C in summer for panting (HT_RH$_p$) and increased metabolism (HT_RH$_m$), respectively. We also flagged any ambient temperature value in the summer that exceeded the thresholds of McCann et al. (2013) of 17 °C (HT_MCm_nowind) and 24 °C (HT_MCm_wind) for increased metabolism in windless or windy conditions, respectively.

We defined Heat Days (HTD) as days where at least one of the ambient temperature values exceeded published thresholds shown to induce panting or increased metabolism in summer and winter. We coded HTDs according to the same 4 thresholds: the Renecker and Hudson (1986) thresholds for increased metabolism (HTD_RH$_m$) or panting (HTD_RH$_p$) and the McCann et al. (2013) thresholds with (HTD_MC$_m$_wind) and without wind (HTD_MC$_m$_nowind). Normal T$_b$ of moose ranges from 38.4 to 38.9 °C (101.1–102 °F; Franzmann et al. 1984); therefore, we assumed a moose to be above normal by adding 0.27 °C (0.5 °F) to the high end of the range. This small buffer also accounts for a slight bias of the MIT to be 0.03 °C lower, on average, than vaginal implant-derived T$_b$ of moose (Herberg et al. 2018). We defined a "hot moose day" (HMD) as a day with at least one MIT-derived temperature ≥ 39.17 °C. In addition to "flagging" days as above or below these thresholds, we also compiled the maximum daily T$_b$ for each moose, as well as the daily number of readings ≥ 39.17 °C. A hot moose

Table 1. Seasonal start and end dates from 2013–2017 for moose in northeast Minnesota.

Year	Winter Start[1]	Winter End[1]	Spring Start[2]	Spring End[2]	Summer Start[3]	Summer End[3]	Fall Start[4]	Fall End[4]
2013	study started	4/24/2013	4/25/2013	6/2/2013	6/3/2013	10/14/2013	10/15/2013	12/2/2013
2014	12/3/2013	4/21/2014	4/22/2014	6/6/2014	6/7/2014	10/6/2014	10/7/2014	12/19/2014
2015	12/20/2014	3/10/2015	3/11/2015	6/1/2015	6/2/2015	10/9/2015	10/10/2015	12/18/2015
2016	12/19/2015	3/25/2016	3/26/2016	6/1/2016	6/2/2016	10/20/2016	10/21/2016	11/30/2016
2017	12/1/2016	2/24/2017	2/25/2017	6/2/2017	6/3/2017	10/14/2017	Study ended	

[1] Start and end dates of winter were determined as the dates when the average snow depth across 10 snow depth stations was consistently more than 4 inches.

[2] Spring starts the first day after the end of winter and ends the last day of parturition (Severud et al. 2015).

[3] Summer starts the first day after the end of winter and ends a day prior to the start of fall[4].

[4] Start of fall based on the date at which the average temperature across three National Oceanic and Atmospheric Administration (NOAA) weather stations falls below freezing (0°C) and ends a day prior to the start of winter[1].

event (HME) was defined as ≥ 2 consecutive $T_b \geq 39.17$ °C. If only one value was above the heat threshold, that HME event consisted of a single observation. We calculated the duration of a HME by subtracting the timestamps between the start and end of the HME and added a correction factor of 5 or 7.5 min depending on the frequency of MIT-derived readings (e.g., 10- or 15-min intervals). Because we did not know exactly when T_b returned to normal within an interval, adding a small correction factor ensured that we did not have HME events that last 0 minutes (in the case when it is only 1 event), and accounted for that uncertainty.

Although HME is a good indication that T_b was above normal, the type of HME can vary widely in both duration and magnitude (e.g., the number of degrees above normal). Therefore, we categorized each HME into two sets of mutually exclusive categories (moderate vs. severe and acute vs. chronic) to better delineate the variation among HMEs. For magnitude, if an HME had a maximum MIT-derived temperature ≥ 39.17 °C but < 39.44 °C, it was defined as moderate; if the maximum was ≥ 39.44 °C (which added 0.54 °C [1.0 °F] to the high end of the normal range), it was classified as severe. For duration, an HME < 35 min was classified as acute and if > 35 min was classified as chronic.

To better understand the time of day moose were most frequently hot in summer, we calculated the distribution of hot T_b across the 24-h day. For each moose, we compiled the total number of T_b readings ≥ 39.17 °C in summer (all years combined) and calculated the percentage that occurred by hour of day.

Statistical Analyses

We fit a first series of models to assess if there were significant differences in the percentage of HMDs across seasons, and if these differences varied by sex or age class using mixed-effect models with a random effect of Animal ID to account for the repeated measures of a given moose, and Year to account for annual variation (Table 2). We then fit a second series of models to test the overall effect of ambient temperature on T_b. We fit 4 different mixed-effect models; each contained a random effect for Year to account for annual variation not captured in the data and Animal ID to account for variation across individuals. The first two models were linear mixed effect models with maximum daily T_b as measured by the MIT (maxMit) as a response; the explanatory variable was either 1) maximum daily ambient temperature (maxTemp) or 2) a binary variable (1-0) that characterized whether a day was defined as a Heat Day (1-0) based on the different ambient temperature thresholds defined above (HTD_RH_m, HTD_RH_p, $HTD\_MC_m\_wind$, $HTD\_MC_m\_nowind$). The third and fourth models were generalized mixed-effect models (binomial family with logit link function) with a binary response variable (0-1) that represented whether a day was characterized as a HMD for a given moose (Table 2). We included an autoregressive term for the errors (AR1) in the aforementioned models.

We tested whether wind speed modified the relationship between maximum daily T_b and ambient temperature in the summer by adding an interaction term for a) maximum daily wind speed (mph), b) mean daily wind speed (mph), or c) whether or not the average daily wind speed was > 11.37 mph, the experimental wind speed of McCann et al. (2013).

Moose Survival as a Function of Heat Stress

Our objective was to evaluate whether heat stress as we defined above impacted moose survival over the course of a year. By organizing the data of individual moose into

Table 2. List of fitted regression models including the dependent variable and independent covariates, which season was included, and if a random intercept was included, northeast Minnesota, 2013–2017.

Dependent variable	Covariate (s)	Season (s)	Random intercept
%HMDs[1]	Season	All	Animal ID / Year
%HMDs	Season * Sex (males)	All	Animal ID / Year
%HMDs	Season * Age class (young, prime, old)	All	Animal ID / Year
maxMIT[2]	Maximum daily ambient temperature (maxTemp)	Summer	Animal ID / Year
maxMIT	Heat Day (HTD=1 or 0)[6] i) HTD_RHm, ii) HTD_RHp, iii) HTD_MCm_wind, iv) HTD_MCm_nowind	Summer	Animal ID / Year
HMD[3]	maxTemp[7]	Summer	Animal ID / Year
HMD	Heat Day (HTD=1 or 0) i) HTD_RHm, ii) HTD_RHp, iii) HTD_MCm_wind, iv) HTD_MCm_nowind	Summer	Animal ID / Year
Moose-year survival[8]	Mean moderate[9] HME events/day	All	None
Moose-year survival[8]	Mean severe[10] HME events/day	All	None
Moose-year survival[8]	Mean acute[11] HME events/day	All	None
Moose-year survival[8]	Mean chronic[12] HME events/day	All	None
Moose-year survival[8]	Mean moderate HME events/day + Mean acute HME events/day	All	None
Moose-year survival[8]	Mean severe HME events/day + Mean acute HME events/day	All	None
Moose-year survival[8]	Mean moderate HME events/day + Mean chronic HME events/day	All	None
Moose-year survival[8]	Mean moderate HME events/day + Mean chronic HME events/day	All	None

[1] Percentage of days where, for a given moose and within a given season, at least one of the T_b values (as measured with the mortality implant transmitters [MITs]) was above or equal to 39.17°C.

[2] Maximum daily T_b as measured by the MITs for a given moose.

[3] Binary response variable to categorize a day as Hot Moose Day (1) (i.e., when a moose had at least one MIT value above or equal to 39.17) or not (0).

[6] Binary explanatory variable to categorize whether or not a day was above one of the heat thresholds (HTD=1) or not (0). Heat thresholds are HT_RH_m = -2.2°C in winter and 14°C in summer thresholds for increased metabolism in captive moose (Renecker and Hudson 1986), HT_RH_p = -5.1°C in winter and 20°C in summer threshold for panting in captive moose (Renecker and Hudson 1986), HTD_MCm_nowind = 17°C in summer for increased metabolism in captive moose (McCann et al. 2013), and HTD_MCm_wind = 24°C in summer for increased metabolism in captive moose (McCann et al. 2013).

[7] Maximum daily ambient temperature.

[8] Interval survival of moose from the first day of summer until the last day of spring (moose-year).

[9] Moderate hot moose event (HME) = maximum MIT-derived temperature of HME ≥39.17°C but <39.44°C.

[10] Severe HME = maximum MIT-derived temperature of HME was ≥39.44°C.

[11] Acute HME = HME duration <35 minutes

[12] Chronic HME = HME >35 minutes.

moose-years (e.g., moose-year 2013 ran from the 1st day of summer [3 June 2013] until the last day of spring [6 June 2014]), we created 63 discrete moose-years of data. We only used data from 3 June 2013 (start of moose-year 2013) through 2 June 2017 (end of moose year 2016). We treated each moose-year independently to evaluate the possible impact of heat stress occurring within a given moose-year. This approach could not account for any potential cumulative effects of repetitive heat stress across multiple moose-years.

To understand the cumulative heat loads on survival for the entire moose-year, we calculated the average number of HMEs per day. We summed the total number of HMEs of each type (moderate, severe, acute, and chronic) for the entire time a moose was alive within a moose-year, and then divided it by the number of days each moose was alive to account for any mortality. We then compared the average (± 95% bootstrapped confidence intervals) daily rate of the HME types between surviving and dead moose in that moose-year. We used bootstrapped confidence intervals because the average HME/day data were right-skewed.

We also fit univariate and bivariate logistic regression models (binomial family with logit link) with survival as a binary response variable (1 for moose that died and 0 for moose that survived the entire moose-year; logit link) and HME type as the predictor variables for the full moose-year data. We fit univariate logistic regression models for each HME type (i.e., univariate models) and each possible bivariate model combination of HME type (e.g., moderate-acute, moderate-chronic, etc.; Table 2) as additive (e.g., moderate + acute) and tested for interactions between the two variables. We compared relative support of the models using AICc (Burnham and Anderson 1998). For each model, we also fit a sex (male or female) and age class (young, prime, or old) *ad hoc* to determine if any of these variables had an effect on survival after accounting for heat loads. We calculated Nagelkerke's R^2 for each model to understand the variation explained by the heat stress variables included in our models. We visualized results from the best-supported model by back-predicting the survival probabilities against the original range of the explanatory variable (e.g., moderate HMEs/day in the sample = 0.06–2.07). We selected that prediction range to limit our inference to the values observed and account for the full range of values within the dataset.

All data visualizations and statistical analyses were conducted in R (R Core Team 2023) with the AICcmodavg (Mazerolle 2023), boot (Canty and Ripley 2024), ggplot2 (Wickham 2016), MASS (Venables and Ripley 2002), MuMIn (Bartoń 2023), and nlme (Pinheiro and Bates 2000, Pinheiro et al. 2023).

RESULTS

Ambient Temperature Thresholds

During the 5 years of our study, summer ambient temperatures were above the RH_m and RH_p thresholds 86–93% and 61–72% of days, and above the MC_m_nowind and MC_m_wind thresholds 77–85% and 27–41% of days, respectively (Table 3, Fig. 2a). Similarly, most winter days (38–69%) were above the RH_m threshold, while 23–51% of winter days exceeded the RH_p threshold (Table 3, Fig. 2b). During these years, moose experienced HTD days above RHm and RMp threshold 81.8–92.5% and 49.3–67.5% of the summer seasons, and 49.2–78.5% and 36.3–60.2% of winter seasons, respectively (Fig. 3). Moose also experienced HTD days above MC_m_nowind and MC_m_wind thresholds 71.9–83.4% and 17.1–37.5% and of

Table 3. Seasonal variations in ambient temperature compiled across eight Remote Automatic Weather Stations (RAWS) in northeast Minnesota, 2013–2017, and the percentage of days that exceeding published ambient temperature thresholds for heat stress in moose (*Alces alces*), called a Heat Day (HTD).

Season	Year	Avg % HTD RHm[1]	Avg % HTD RHp[2]	Avg% HTD MCm_ Nowind[3]	Avg% HTD MCm_ Wind[4]	Max (°C)	Min (°C)
Summer	2013	91.57	65.07	84.26	31.59	33.33	-4
	2014	86	61.1	77.04	26.64	35	-3
	2015	92.58	72.45	85.08	40.96	34	-6.11
	2016	90.42	67.45	81.83	34.85	33.33	-5
	2017	90.09	62.56	77.47	33.77	33	-5
Winter	2012–13	68.79	51			14	-38.33
	2013–14	38.09	30.27			17.78	-40.56
	2014–15	39.96	23.36			17	-38.89
	2015–16	67.6	47.05			25	-34.44
	2016–17	55.38	40.98			17.22	-38.33

[1] HT_RH_m = -2.2°C in winter and 14°C in summer thresholds for increased metabolism in captive moose (Renecker and Hudson 1986).
[2] HT_RH_p = -5.1°C in winter and 20°C in summer threshold for panting in captive moose (Renecker and Hudson 1986).
[3] HTD_MCm_nowind = 17°C in summer for increased metabolism in captive moose (McCann et al. 2013).
[4] HTD_MCm_wind = 24°C in summer for increased metabolism in captive moose (McCann et al. 2013).

summer days, respectively (Fig. 3). We found no effect of wind on maximum daily T_b of moose during summer at scales we were able to measure.

Hot Moose Days (HMD)

Of 41 moose, 3 animals never experienced an MIT-derived temperature reading ≥ 39.17 °C; all other 38 animals experienced at least one HMD and most (i.e., 37 animals) experienced an HMD with at least one chronic or one severe event. The range of above normal T_b was 39.17 to 41.46 °C. Moose were most often hot in the evenings and overnight, as 76% of hot T_b occurred between 18:00–6:00 hr (40% between 18:00–24:00 and 36% between 00:00–06:00 hr) in summer (Fig. 4). The number of HMEs varied seasonally, with summers having the most events across all animals (mean = 2,364 events, range = 1,276–3,991 across years; Table 4). The mean duration of HMEs during four summers varied from 16 (SE = 0.5) to 44.4 min (SE = 1.2), ranging from 5 to 1,065 min (Table 4). The percentage of HMDs varied significantly among seasons (p <0.001), with moose exhibiting the highest percentage of HMDs in the summer (overall mean across all years and individuals = 47% HMDs, SE = 2.6), followed by spring (mean = 8.9%, SE = 1.0), fall (mean = 3.46, SE = 0.8), and winter (mean = 0.7%, SE = 0.6) (Fig. 5). Sex or age class alone did not explain the overall variations in the percentage of HMDs across the entire dataset, but both sex and age class significantly influenced the differences in the percentage of HMDs across seasons (p = 0.0019 and p <0.0001 for the interaction between season and sex, and season and age class, respectively). Sex was only significant in summer, with males experiencing a higher percentage of HMD than females (p <0.001). Young moose were also more likely (p <0.001) to

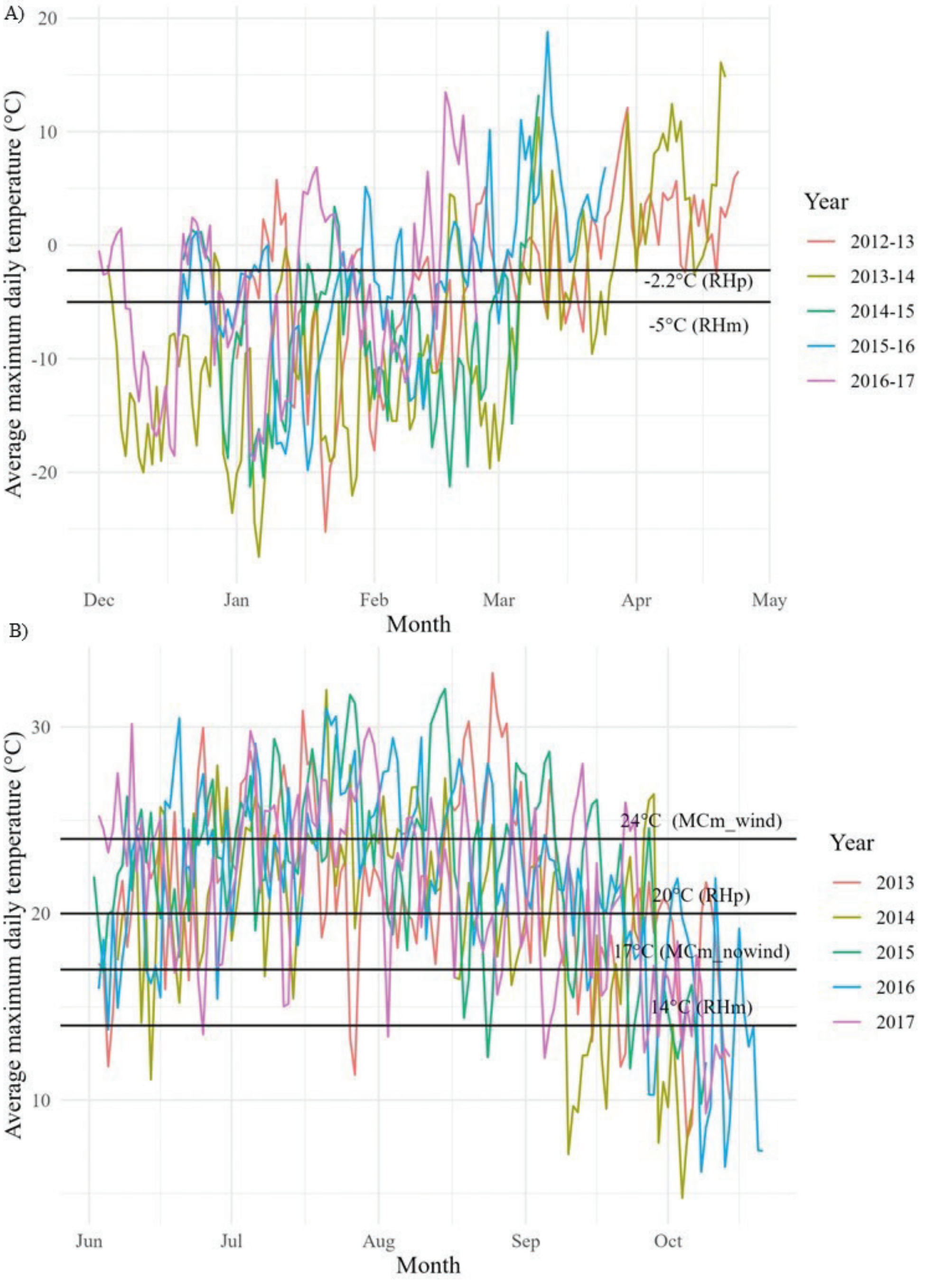

Fig. 2. Seasonal variability in maximum daily temperature (°C) across A) summer and B) winter, averaged across eight Remote Automatic Weather Stations located throughout the moose range in northeast Minnesota, 2013–2017. The horizontal lines correspond to previously published ambient temperature thresholds shown to induce heat stress in captive moose, including: ($\mathrm{MC_m}$_wind (increased metabolism with a constant wind of 11.37 mph) and $\mathrm{MC_m}$_nowind (increased metabolism under no wind), McCann et al. (2013); $\mathrm{RH_m}$ (increased metabolism) and $\mathrm{RH_p}$ (panting), Renecker and Hudson (1986).

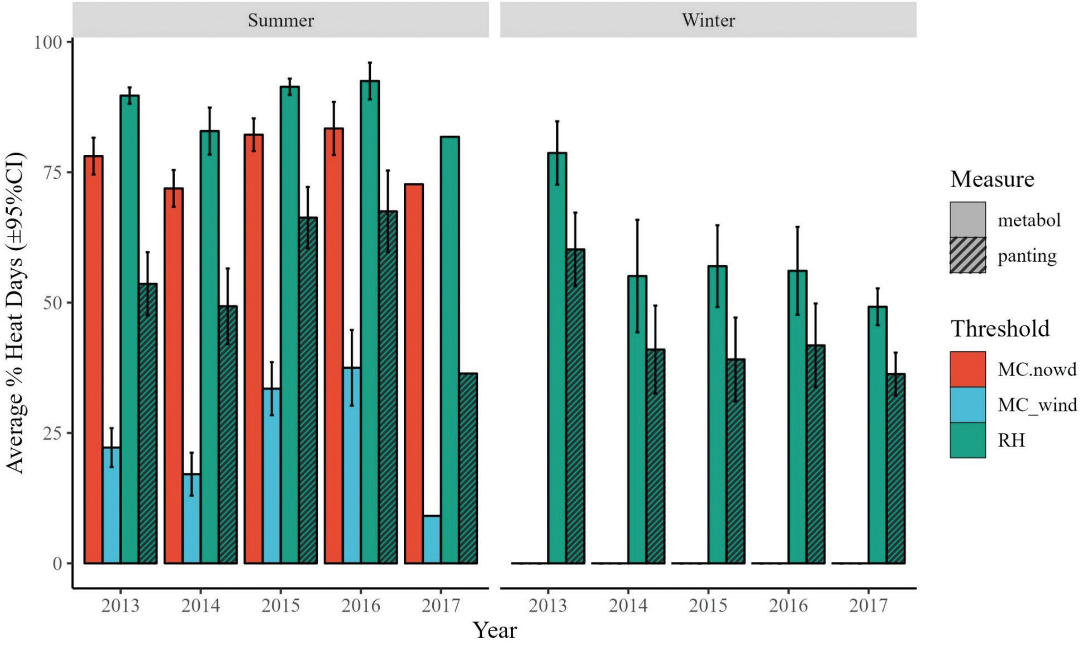

Fig. 3. Average (95%CI) percentage of days moose experienced ambient temperatures above previously published thresholds (defined as a heat day [HTD]) shown to induce heat stress, during summer and winter seasons, 2013–2017, northeast Minnesota. A moose experienced a HTD if the maximum daily ambient temperature recorded at the weather station nearest its location was above one of the published heat thresholds that shown to induce increased metabolism (metabol) or panting: MC_wind (increased metabolism with a constant wind of 11.37 mph) and MC.nowind (increased metabolism under no wind) (McCann et al. 2013), RH (Renecker and Hudson 1986).

experience a HMD in summer compared to prime-aged and old animals.

Ambient Temperature Effects

On average, maximum daily T_b increased (Intercept = 38.81 (95% CI: 38.75–38.88), slope = 0.016 (95% CI = 0.014–0.018), p <0.001) with increasing maximum daily ambient temperature in summer; however, substantial individual variation existed in the population trend (Conditional R^2 = 0.19) (Fig. 6). Based on a 95% confidence interval, our fitted model predicts a moose will experience above normal T_b or HME at least once on days when the maximum daily ambient temperatures is ≥ 25 °C in summer (Fig. 6). The probability of a HMD also increased with increasing ambient temperature (p <0.001, Conditional R^2 = 0.24) in summer, and a moose was more likely (p <0.001) to experience a HMD on a day defined as a HTD with odds ratios varying between 1.79 and 2.76 (Conditional R^2 = 0.15–0.16). We were unable to fit a model of HMD as a function of HTD in winter due to the rarity of HMDs.

Heat Stress Impact on Moose Survival

Of the total number of HMEs observed throughout the study (n = 10,755), the majority were of acute duration (77%) and moderate magnitude (73% Chronic (23%) and severe HMEs (27%) occurred less frequently and primarily in the summer season. We found considerable variation among individuals in the average daily rate of HMEs in a moose-year. Beyond this variable HME

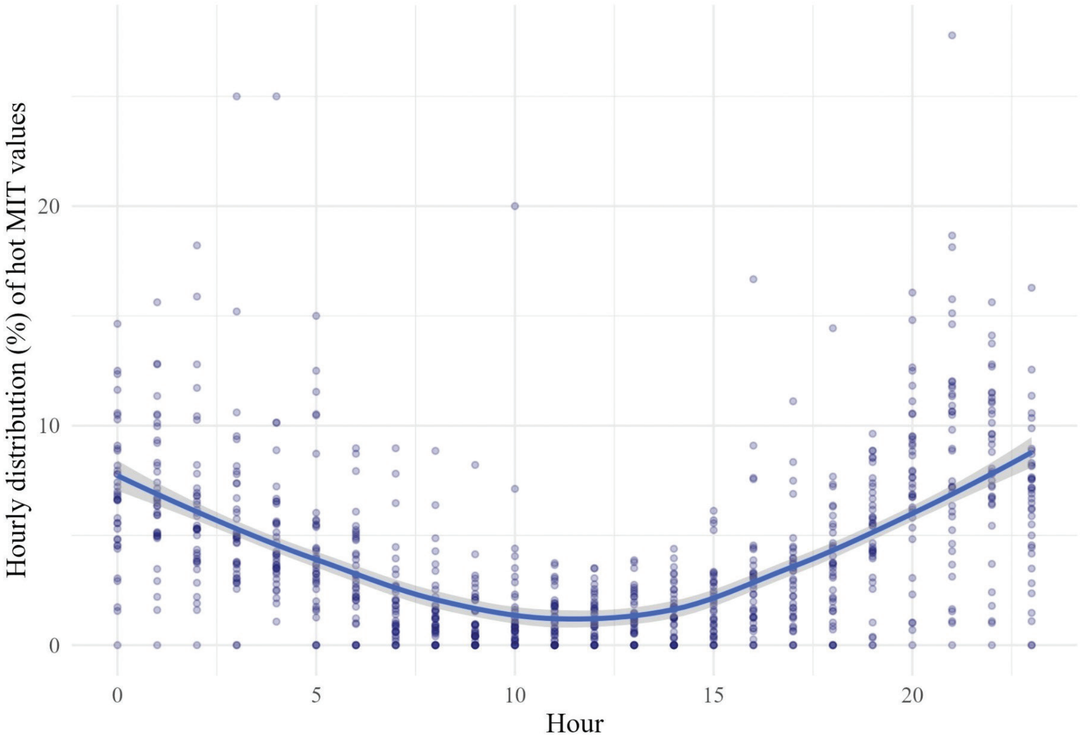

Fig. 4. Hourly distribution (%) of individual moose T_b ≥39.17 °C during summers, 2013–2017, northeast Minnesota. A smooth regression line (blue) is included to show the general pattern with 95% confidence intervals (grey).

data, only a small proportion of moose died (14 deaths in 63 moose-years of data or 3 per year); most deaths (8) occurred in summer, 4 in winter, and 1 each in fall and spring. The proximate cause of death was determined in a companion project of cause-specific mortality and included infection (n = 5), wolf predation (n = 4), parasites (n = 3), vehicle collision (n = 1), and undetermined (n = 1) (Carstensen et al. 2017)

For the full moose-year data, moose that died had 2.0–2.8 times higher average HMEs per day (mean daily rate ranged from 0.32–0.96 among different HME types; Table 5) than surviving moose for all HME types (mean daily rate ranged from 0.16–0.46 among different HME types; Table 5); however, the associated confidence intervals were quite wide. By moose-year, moose that died had 1.3–4.9 times more HMEs per day on average (mean daily HME rates ranged from 0.10–1.63 among different HME types; Table 6) than moose that survived (mean daily HME rates ranged from 0.04–0.54 among different HME types; Table 6); however, only a few moose-year/HME type combination pairs were statistically different because the confidence intervals overlapped in most cases (Table 6).

Neither sex or age class were statistically significant ($p > 0.05$) relative to survival in the regression models and were dropped from the final models. We also found no interactions between any of the parameter combinations in the bivariate models, and dropped the interaction terms and fit simpler, additive models. Our model selection results indicated the average number of moderate HMEs per

Table 4. Occurrence and duration of above normal T_b (≥39.17°C) in wild moose (*Alces alces*) in northeast Minnesota, 2013–2017. We defined days with T_b ≥39.17 °C as a Hot Moose Day (HMD) and their occurrence as a Hot Moose Event (HME).

Season	Year	N[1]	N HME[2]	Mean # days[3]	Mean % (SE) HMD[4]	N moose (%) HMD[5]	Mean # (SE) HME	Mean duration (min) (SE) HME	Range of duration (min) of HME
Spring	2013	13	66	37.6	8.0 (1.7)	12 (92)	5.1 (1.0)	21.0 (2.5)	5 – 98
	2014	18	266	43.7	11.0 (1.9)	16 (89)	14.8 (4.1)	20.1 (1.7)	5 – 173
	2015	25	311	77.9	8.0 (1.8)	21 (84)	12.4 (3.8)	38.5 (4.1)	5 – 745
	2016	13	174	64.6	11.4 (2.4)	13 (100)	13.4 (3.5)	44.4 (6.2)	5 – 796
	2017	5	1	28.4	0.3 (0.3)	1 (20)	0.2 (0.2)	5	5 – 5
Summer	2013	12	1276	115.1	43.6 (5.6)	12 (100)	106.3 (15.4)	16 (0.5)	5 – 128
	2014	18	2641	99.8	44.7 (4.6)	17 (94)	146.7 (27.6)	17.3 (0.4)	5 – 245
	2015	23	3991	120.1	50.4 (4.4)	23 (100)	173.5 (26.5)	44.4 (1.2)	5 – 1065
	2016	11	1550	120.8	49.7 (5.9)	11(100)	140.9 (20.0)	37.4 (1.3)	5 – 645
	2017	1	0	11.0	0.0	0	0.0		
Fall	2013	10	2	42.0	0.2 (0.2)	1 (10)	0.2 (0.2)	5 (0)	5 – 5
	2014	14	134	67.7	2.3 (1.0)	8 (57)	9.6 (6.0)	18.5 (1.8)	5 – 113
	2015	19	234	67.8	6.2 (1.7)	14 (74)	12.3 (5.7)	85.3 (8.6)	5 – 775
	2016	7	9	41.0	2.8 (1.4)	4 (57)	1.3 (0.6)	20.6 (5.0)	5 – 45
Winter	2012–13	14	17	73.9	0.4 (0.2)	3 (21)	1.2 (1.1)	19.8 (3.9)	8 – 53
	2013–14	21	71	90.0	0.7 (0.5)	5 (24)	3.4 (2.4)	22.5 (2.5)	5 – 95
	2014–15	30	5	36.0	1.2 (0.8)	3 (10)	0.2 (0.1)	15.1 (6.6)	5 – 38
	2015–16	18	5	82.0	0.3 (0.2)	3 (17)	0.3 (0.2)	55 (38.7)	5 – 205
	2016–17	7	2	79.3	0.4 (0.4)	1 (14)	0.3 (0.3)	5 (0)	5 – 5

[1] Number of moose being monitored during each season and year.

[2] Total number of Hot Moose Events (HME)

[3] Average number of days N moose were monitored in a given season and year.

[4] Average percentage of Hot Moose Days (HMD) moose experienced across all moose in a given season and year.

[5] Total number (N moose) and percentage of moose that had at least one HMD in a given season and year.

day was a significant variable. It showed up in the top three model results (all within 2.16 ΔAICc) which carried 73% of the cumulative weight (Table 7). Of the bivariate models, the magnitude variables seemed to rise to the top, but under closer inspection these are likely less informative parameters due to the significant amount of variation in HMEs in the dataset (Arnold 2010). Of the top three models, only the univariate moderate model had a significant slope parameter ($\beta = 2.31$, 95% BCI = 0.80–3.84) and was most parsimonious (Fig. 7). There was considerable variation in the top model (univariate moderate model) and very little of the overall variation in moose survival was explained by just the heat parameter (Nagelkerke's $r^2 = 0.18$). In that model, for an average increase of 1 acute HME per day, the odds of a moose dying increased by 9.99 (95% CI: 1.98–38.27). Because the daily means were relatively low and an increase of 1 moderate unit per day would be rather large, we divided the regression parameter and bootstrapped

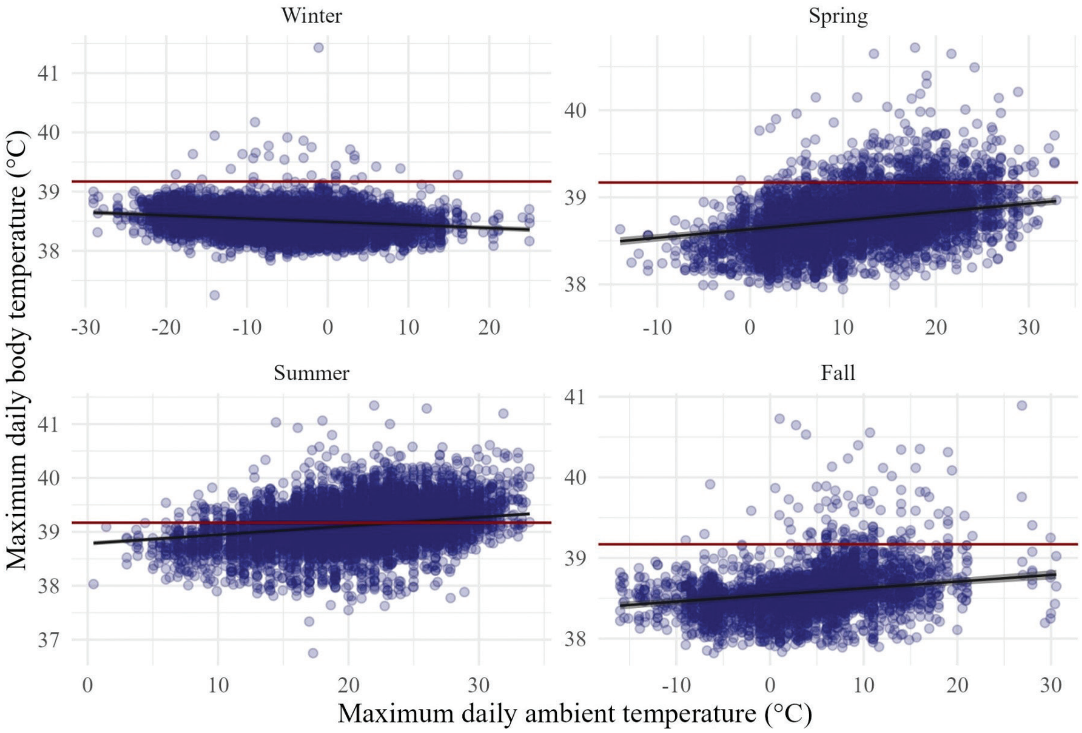

Fig. 5. Maximum daily T_b of moose as a function of maximum daily ambient temperature they experienced across all seasons, 2013–2017, northeast Minnesota. The red line indicates the T_b at which moose may begin to experience heat stress symptoms (39.17 °C). The black lines represent the predicted regression line (95%CI) from the modeled relationship of maximum daily T_b versus maximum daily temperature with animal ID and year as random intercepts.

confidence intervals by 7 to mimic the effects of increasing a moderate HME per week on survival. On average, the odds of a moose dying were 1.42 times higher (95% CI: 0.28–5.47) for each increase of 1 moderate HME per week.

DISCUSSION

We found moose in Minnesota are more likely to experience heat stress during summer than winter. In contrast, Lenarz et al. (2009) hypothesized that ambient temperatures above the critical threshold of -5 °C in January caused heat-stress and lower probability of survival. However, when exposed to ambient temperatures exceeding this threshold for over half of the winter seasons, T_b was rarely elevated in our study moose; conversely, HME and HMD events were common in summer. While we found moose were more likely to be hot when ambient temperature was above the two published summer thresholds (Renecker and Hudson 1986, McCann et al. 2013), this was likely less related to a biological relevance of the static thresholds and more likely attributed to moose exposed to heat days nearly the entirety of the summer seasons (77.0–92.6% and 61.1–72.5% of the time above thresholds for increased metabolism and panting, respectively). The significant relationship between the hottest summer days and an HME is critically important to consider because climate models predict the average summer temperature will increase 5–6°C across Minnesota by the end of the 21st century (MNDNR 2016).

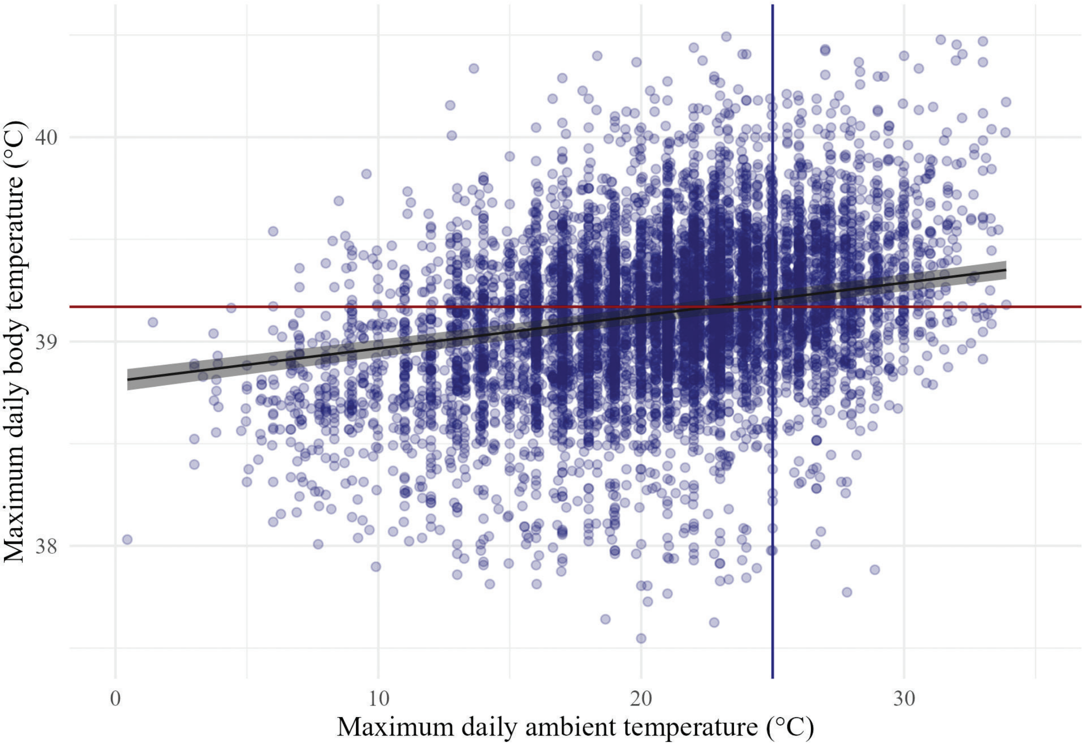

Fig. 6. Maximum daily T_b of moose as a function of the maximum daily ambient temperature they experienced during summers 2013–2017, northeast Minnesota. The red line indicates the T_b at which moose may begin to experience heat stress symptoms (39.17 °C). The black lines represent the predicted regression line (95%CI) from the modeled relationship of maximum daily T_b versus maximum daily temperature with animal ID and year as random intercepts. The blue vertical line represents the ambient temperature (25 °C) above which our regression model predicts that a moose will begin experiencing heat stress symptoms.

Table 5. Average number of daily hot moose events (± 95% bootstrapped confidence intervals) for moose (*Alces alces*) that died or survived for a moose-year (1st day of summer-last day of spring) in northeast Minnesota, 2013–2017.

	Moose that survived (n = 49)		Moose that died (n = 14)	
Type of hot moose events	$\bar{X}$/day	(bootstrapped CI)	$\bar{X}$/day	(bootstrapped CI)
Acute*	0.46	(0.37–0.54)	0.95	(0.56–1.35)
Chronic	0.12	(0.09–0.16)	0.33	(0.15–0.57)
Moderate*	0.42	(0.35–0.50)	0.96	(0.61–1.35)
Severe	0.16	(0.13–0.19)	0.32	(0.18–0.46)
All types combined*	0.58	(0.48-0.68)	1.28	(0.82-1.79)

*denotes statistical significance at the α=0.05 level.

Our model predicts that moose may experience heat stress symptoms (as defined by elevated T_b) in summer when daily ambient temperature is ≥ 25 °C, a threshold higher than reported by Renecker and Hudson (1986) and McCann et al. (2013). Interestingly, the highest

Table 6. Average number of daily hot moose events (± 95% bootstrapped confidence intervals; BCI) for moose (*Alces alces*) that died or survived for each moose-year (1st day of summer-last day of spring) in northeast Minnesota, 2013–2017.

		Surviving moose (*n* = 49)				Moose that died (*n* = 14)			
Type of HME	Moose year	N	Mean number HME/day	95% Lower BCI	95% Upper BCI	N	Mean number HME/day	95% Lower BCI	95% Upper BCI
Acute	2013	9	0.29	0.22	0.37	3	1.01	0.19	2.24
	2014	14	0.54	0.40	0.71	3	1.31	0.12	2.30
	2015	17	0.46	0.33	0.62	6	0.62	0.32	0.97
	2016	9	0.48	0.29	0.71	2	1.29	0.81	1.77
Chronic	2013	9	0.04	0.03	0.06	3	0.22	0.05	0.49
	2014	14	0.08	0.05	0.13	3	0.10	0.03	0.16
	2015	17	0.17	0.09	0.26	6	0.33	0.08	0.70
	2016	9	0.17	0.12	0.23	2	0.86	0.69	1.03
Moderate	2013	9	0.25	0.19	0.33	3	0.91	0.16	2.04
	2014	14	0.42	0.29	0.57	3	1.06	0.13	1.82
	2015	17	0.47	0.34	0.62	6	0.71	0.32	1.24
	2016	9	0.49	0.31	0.70	2	1.63	1.19	2.07
Severe	2013	9	0.08	0.04	0.11	3	0.33	0.07	0.69
	2014	14	0.20	0.13	0.27	3	0.35	0.02	0.63
	2015	17	0.17	0.12	0.23	6	0.24	0.09	0.45
	2016	9	0.16	0.11	0.22	2	0.52	0.31	0.73

Table 7. Model selection results for the effect of average daily number of hot moose event types within entire moose year (1st day of summer to last day of spring) on annual moose (*Alces alces*) survival in northeast Minnesota, 2013–2017. We calculated Nagelkerke's R^2 values for the univariate models and Nagelkerke's adjusted R^2 values for the bivariate models.

Model	K	AICc	Δ AICc	AICc Weight	Cumulative weight	-log-likelihood	Nagelkerke's R^2
Moderate	2	58.22	0.00	0.42	0.42	-27.01	0.18
Moderate-Acute	3	59.98	1.76	0.17	0.59	-26.79	0.28
Moderate-Chronic	3	60.38	2.16	0.14	0.73	-26.98	0.28
Acute	2	60.91	2.69	0.11	0.84	-28.36	0.15
Severe	2	62.39	4.17	0.05	0.89	-29.10	0.13
Chronic	2	62.95	4.73	0.04	0.93	-29.38	0.12
Severe-Acute	3	63.12	4.90	0.04	0.97	-28.36	0.22
Severe-Chronic	3	63.43	5.21	0.03	1.00	-28.51	0.21

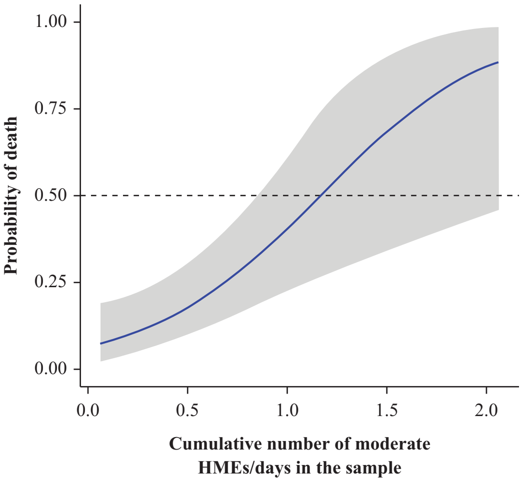

Fig. 7. Effect of average daily number of moderate HMEs within entire moose year (1st day of summer to last day of spring) on annual moose (*Alces alces*) survival probability in Minnesota, 2013–2017.

McCann et al. (2013) threshold (24 °C) was measured in constant wind speed of 11.3 mph and was 7 °C higher than in windless conditions. We were unable to account for the effect of wind on our individual animals but recognize that wind speed varies spatially and by elevation, cover type, and time-of-day (McCann et al. 2016), and often aids thermoregulation. Environmental variation, common thermoregulatory behaviors of moose, and the large variation in individual response (Fig. 6) all refute the use of a static threshold of ambient temperature as predictive of heat stress in moose. As Mitchell et al. (2018) and Thompson et al. (2019) cautioned, use of such thresholds may be misleading and are not intended for direct field application (Pekins 2020).

The diurnal pattern of T_b, with evening peaks and dissipation of excess heat overnight, was similar to trends reported for ruminants in northern latitudes (Signer et al. 2011, Thompson et al. 2019, Græsli et al. 2022), as well as desert ungulates (Fuller et al. 1999, Mitchel et al. 1997, Maloney et al. 2002). However, in our study the magnitude and duration of daily elevation of T_b were unique. Semi-captive Alaskan moose exhibited a daily rhythm (range = 0.9 °C) in core T_b in summer without predicted heat stress, with T_b peaking at 21:00 hr (Thompson et al. 2019). Our moose peaked somewhat later in the day (24:00 hr) and were slower to dissipate excess heat, as 36% of elevated T_b occurred from 0:00 to 6:00 hr. However, because daylight and time-of-day affect foraging activity that elevates T_b, the disparate daylight conditions in these two regions confound direct comparisons, and we could not account for daily foraging activity and movement that influence daily patterns of T_b in these analyses. Possibly, physiological ability to mitigate heat stress differs in moose living at the southern extent of their bioclimatic range and more northern populations.

The gut flora of ruminants is heat sensitive and does not survive long durations of temperatures > 40 °C (Hungate 1966). Adverse effects of heat stress in the rumen of cattle include lower gut motility, rumination, and depressed appetite, effectively reducing intake and digestibility of forage (Yakav et al. 2013). Beale et al. (2018) hypothesized that elevated summer body temperatures that reduce forage digestibility could negatively impact metabolism, energetics, and ultimately survival. It is possible that heat loads we observed in some individual moose during summer are reducing digestibility of even high-quality forage, which can negatively impact metabolism, energetics and ultimately survival (Beale et al. 2018). Overall, however, the average summer HME (i.e., 32 min) was less than acute by our definition (35 min), and of moderate magnitude (< 39.44 °C), although a few individual HMEs extended several hours (longest = 17.7 h). The lack of chronic and severe HMEs is perhaps unsurprising given the environmental variation, behavioral choices, and mobility of moose to maintain T_b within a mostly 2-degree C range, as documented in Alaska (Thompson et al. 2019).

The maximum T_b we recorded was 41.5 °C and higher than that (40.8 °C) measured with a MIT in a wild moose hunted with dogs in Sweden (Græsli et al. (2020*b*). While unable to account for frequency and duration of predator encounters experienced by moose in our study, it is likely that certain HMEs reflected predator interactions. Wolves were abundant in our study area and accounted for approximately a third of adult moose deaths (Carstensen et al. 2017). For example, one moose that was killed by wolves in summer had a rapid increase in T_b from 38.6 to 41.3 °C coincident with a 618 m movement just prior to its death (Carstensen, unpublished data), indicating that a wolf encounter can induce acute and severe increase in T_b. Further, such increases in T_b might adversely affect survival due to cytotoxicity as damage to mammalian cells from hyperthermia begins in a relatively short period of elevated T_b (> 40–41°C). The extent of damage is dependent on exposure time and other stress factors but might result in organ failure and death (Lepock 2003, Tansey and Johnson 2015). If hunting moose with dogs can cause a notable stress event despite increased resting times, and possibly cause adverse effects to reproduction and body condition (Græsli et al. 2020*b*), it's plausible that a similar response might occur from extended chases in moose-wolf encounters.

We found a relationship between HME and survival, as moose that died had 2.0–2.8 times higher average HMEs per day over the course of a year, and dead moose had higher mean HMEs of all types compared to survivors. However, our data were highly variable, the sample of dead moose was small and similar annually (n = 2–3, except in 2016), and moderate and acute HMEs were predominant (>73%); chronic (2,492) and severe (2,857) HMEs accounted for only 23–27% of HMEs. Interestingly, we found that despite the low daily rate, having more moderate HMEs may be more problematic for moose than extreme HMEs alone. For each increase of 1 moderate HME per week, the odds of a moose dying increased (0.28 to 5.47 times). While arid-zone ungulates are well adapted to withstand hyperthermic events, such as employing selective brain cooling to conserve body water (Mitchell et al. 2002), moose are maladapted to increasing environmental temperatures (especially hotter summers) given their large body size and insulative winter pelage (Kelsall and Telfer 1974). Perhaps the frequent occurrence of HMEs in summers, although mostly moderate and acute events, has a cumulative survival effect. Our moose-year survival period included the possible direct effect of HMEs within the current summer and later in post-summer seasons (indirect effect). While most deaths occurred during summer (8 of 14), we cannot know if heat stress played a direct role or contributed to stressors (e.g., high parasite loads, poor nutrition, injury) associated with these mortalities.

The leading proximate cause of mortality in this study was infection (36%) that is potentially linked to immunosuppression, co-infection with pathogens or parasites, poor body condition, and attributes of chronic heat stress (Jolles et al. 2015). Murray et al. (2006) found a negative association between moose population change and summer temperature in northwest Minnesota, speculating that heat stress was linked to poor body condition, higher mortality from parasitism and infection, and population decline. Interestingly, the moose in our study with the longest duration (17 h) of a HME in summer was a 6-year old emaciated bull that died mid-winter from a *Pasteurella sp.*

sepsis infection, in concert with severe liver fluke *(Fascioloides magna*)-induced hepatitis, pleuropneumonia, and *Echinococcus sp*. cysts in the lungs. The stress of high heat loads in summer may have affected foraging activity and body condition of this animal by exacerbating the adverse effects of an already high parasite load; however, the cause of the extended HME is unknown. The complexity of teasing out ultimate from proximate causes of mortality must be emphasized as we consider the role that heat stress may play either directly or indirectly in predisposing individual moose to predation risk, parasite exposure, poor body condition, and reduced fitness in context with the larger population. For example, our study population had an average pregnancy rate of 83% and a 30% twinning rate in prime-aged females (Severud et al. 2019) that reflects adequate nutritional condition and good productivity. Yet, this population has declined markedly since 2005 with health-related causes driving the majority of adult moose deaths (Carstensen et al. 2017) and predation suppressing calf survival (Severud et al. 2015).

Numerous studies in North America and Scandinavia reported behavioral responses of wild moose to perceived thermal stress in summer, typically through reduced movement and activity patterns, and selection for thermal shelter (Dussault et al. 2004, Broders et al. 2012, van Beest and Milner 2013, Melin et al. 2014, Street et al. 2015, Ditmer et al. 2017, Montgomery et al. 2019); conversely, others found minimal behavioral response at high ambient temperatures perceived to induce heat stress, and questioned whether heat stress in moose was a population-level concern along their southern border (Lowe et al. 2010, Murray et al. 2012). Common to all these previous studies was the lack of concurrent physiological data to accompany their field observations due to the challenges of obtaining continuous physiological measurements such as core T_b in free-ranging animals. It is possible that the lack of behavioral response by Ontario moose (Lowe et al. 2010) reflected high quality habitat with ample thermal shelter near abundant forage, allowing moose to manage potential thermal stress without making fitness tradeoffs. In Ontario, moose had a high availability of dense mixed-wood stands that simultaneously provided foraging opportunities and thermal cover (Street et al. 2016), whereas Minnesota's moose habitat was dominated by deciduous cover with a more open canopy, potentially leaving them more vulnerable to thermal stress. That said, moose remain highly mobile and are overall habitat generalists, utilizing a wide variety of forage species to their meet nutritional needs. As concern for climate-driven changes to forest composition heightens, the importance of identifying moose habitat prescriptions that maximize both juxtaposition and availability of forage and cover schemes will become central to future moose habitat management.

Here we have demonstrated that elevated T_b in moose is a physiological response to high ambient temperatures in summer, and may influence survival. Future research will explore relationships between the MIT-derived T_b and behaviors of moose, including seasonal and daily habitat use, activity, and movement to identify and assess the role and availability of thermal refugia in the recovery of moose in northeast Minnesota. The influence of climate on moose is often indirect as well, including shifts in forage composition and quality (Soja et al. 2007), reduced calf recruitment (Holmes et al. 2021), range expansion of pathogens and parasites (Repel 2011, Feldman et al. 2017), and increased competition with white-tailed deer (Weiskopf et al. 2019). As global warming heightens, improved understanding of all these relationships and their influence on nutritional condition and productivity of moose will be foundational to future management.

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