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Research Article

Behavioral response of moose *Alces alces* to summer heat stress

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Minnesota moose are heat-stressed during summers, which is adversely impacting their survival. We used both movement and activity data to explore the behavioral responses of Minnesota moose experiencing heat stress, termed 'hot moose events' or HMEs, to understand how both ambient temperature and available habitat contribute to the ability of these moose to thermoregulate. Hot moose ($\geq 39.17^{\circ}\text{C}$, as determined by internal biologgers that continuously recorded body temperature), failed to adopt the behavioral switch to foraging habitats during nocturnal activity displayed by moose maintaining normal body temperatures (i.e. normal moose), which might improve their overall fitness and survival. Hot moose also selected habitats differently than normal moose, including using open canopies that offer little mid-day protection from solar radiation (e.g. ash swamp, meadow marsh bog), whereas normal moose had a stronger selection for thermal refugia. We further investigated the behaviors of moose prone to repeated HMEs within a summer season. Members of this group were majority male, experienced 5× the daily rate of HMEs compared to other hot moose, and were more likely to die. Our findings suggest some moose are making behavioral choices that appear to undermine their ability to thermoregulate on hot summer days, adversely impacting their survival. Individual drivers are likely complex and include both moose health factors and the availability or arrangement of quality forage and cover types. Although we were unable to pinpoint a difference in overall landscape composition between the choices hot and normal moose make, it is likely that fine-scale differences in habitat features, such as patch size, forest structure, and distance to cover, play a key role. Future forest management efforts supporting both thermal and forage needs of moose will help mitigate summer heat stress in populations threatened by climate change.

Keywords: activity, ambient temperature, behavior, body temperature, habitat, Minnesota, mortality implant transmitter, resource selection, thermoregulation



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Introduction

The ability of moose *Alces alces* to thermoregulate in a wide variety of landscapes and climatic conditions has made them adaptable to living in habitats ranging from temperate boreal forests to coastal–boreal landscapes to grasslands and prairie potholes. Their high mobility, combined with a diverse diet that includes a wide variety of forage species, allows moose to function as a habitat generalist more than a specialist (Shipley 2010, Stewart et al. 2010, Koetke et al. 2023, Spitzer et al. 2025). While those traits should bode well for their ability to adapt to a changing climate, moose are also a large-bodied herbivore. As such, their ability to maintain optimal homeothermy may come at a cost in fitness if faced with behavioral choices that reduce efficiency of heat loss during varying environmental conditions (Porter and Kearney 2009, Hetem et al. 2014, Mitchell et al. 2018). Moose populations are declining in portions of their historic southern range in North America and Eurasia, and thermal stress has been implicated as a contributing factor (Murray et al. 2006, Lenarz et al. 2010, Allen et al. 2017, Jensen et al. 2018, Carstensen et al. 2024).

In Minnesota, moose have declined across their historic range, including near extirpation in the northwest during the 1990s, and a 60% decrease in the northeast in the early 2000s, which has stabilized at approximately 4000 animals for the past decade (McGraw 2025). Numerous studies have documented key drivers of these declines, including high parasite loads and predation (Murray et al. 2006, Mech and Fieberg 2014, Wünschmann et al. 2015, Carstensen et al. 2017), yet others suggest the warming climate may be the ultimate driver (Lenarz et al. 2009, 2010). It is certainly possible that both climatic and non-climatic stressors are acting in concert to adversely impact the survival of these large-bodied, cold-adapted mammals; and it may be the rate of change that poses the greatest challenge, as climate models predict the average summer temperature will increase by 5–6°C across Minnesota by the end of the 21st century (Minnesota Department of Natural Resources 2024).

Historically, exploring the relationship between increasing ambient temperatures and heat stress in wild moose has been largely theoretical, relying on extrapolation of static temperature thresholds suggestive of heat stress in captive moose (Renecker and Hudson 1986, McCann et al. 2013) to free-ranging populations. As such, Lenarz et al. (2010) believed warm winters correlated with heat stress for Minnesota moose and were the primary cause of the population decline but lacked any physiological data to support it. Recent studies utilizing biologgers to continuously measure body temperature of wild moose have discounted the validity of these static ambient temperature thresholds to predict heat stress, determined they are misleading, and cautioned against using them to explain moose behavior (Thompson et al. 2020, Carstensen et al. 2024). Armed with actual physiological data, Carstensen et al. (2024) concluded that summer, not winter, was the season in which Minnesota moose experienced heat stress, and body temperature increased significantly with

increasing ambient temperatures. Although these authors documented the frequency, magnitude, and duration of heat stress events that moose experienced during summers, they failed to explore the behaviors of these moose as contributing factors.

Numerous studies across different environmental settings in North America and Europe reported behavioral responses of moose to elevated ambient temperatures in summer, typically through reduced movement and activity patterns, and selection for thermal refugia (Dussault et al. 2004, Broders et al. 2012, van Beest et al. 2012, Melin et al. 2014, Street et al. 2015, Montgomery et al. 2019, Borowik et al. 2020, Verzuh et al. 2021, van der Veegt 2025, Widén et al. 2025). Seeking cover and lowering thermal stress also reduces body mass loss and improves survival (van Beest and Milner 2013, Carstensen et al. 2024). Presumably moose have evolved these behavioral responses to mitigate excess heat and maintain homeostasis, yet why then are Minnesota moose exceedingly hot? Street et al. (2016) reported marked differences in habitat selection patterns in summer between moose in Ontario compared to Minnesota. Ontario moose favored deciduous and mixed-wood forests that likely allow foraging activities to occur across all temperatures and diurnally. However, selection in Minnesota moose was more dependent on time and temperature, indicating potential trade-offs between foraging habitat and thermal cover. These authors concluded that landscape composition and finer-scale configuration of habitats selected in Minnesota produced complex patterns of space use where moose exposed to high summer temperatures were trading fitness for foraging, seeking cover types that provide thermal refugia but sub-optimal foraging opportunities. If true, are the heat stress events experienced by Minnesota moose in summer linked to foraging habitats that lack accessibility to adjacent thermal cover?

In this study, we expand upon the findings of Carstensen et al. (2024), which documented over 10 000 occurrences where moose experienced above-normal body temperatures ($\geq 39.17^{\circ}\text{C}$, termed ‘hot moose events’, HMEs) during five summers derived from biologgers that continuously recorded body temperatures. Using both movement and activity data temporally linked to body temperature, we explore the behavioral responses of moose preceding, during, and after HMEs to better understand how both ambient temperatures and available habitat contribute to the ability of these moose to thermoregulate. Specifically, our objectives included: 1) describing the behavioral state (e.g. resting, foraging, or traveling) of moose preceding, during, and after HMEs using both raw activity data and modeled behaviors; 2) determining the habitats moose are selecting in association with HME events; 3) comparing activity levels and habitat selection when moose experienced HMEs (i.e. ‘hot moose’) to those that maintained normal body temperatures to understand how their choices may relate to thermal stress; and 4) determining if some moose were more prone to repeated HMEs than others and if behavioral differences exist.

Material and methods

Study area and moose captures

From 2013 to 2015, the Minnesota Department of Natural Resources (MNDNR) captured and collared 173 adult (> 1 year old) moose within the 3732.8 km² study area, located between 47°12' and 47°95'N and between 90°33' and 91°72'W in northeast Minnesota (Fig. 1). Moose were fitted with GPS-Iridium collars (Vectronics Aerospace GmbH) and survival was monitored daily for a cause-specific mortality study (Carstensen et al. 2017). A subset of these moose (n=41; 23 females and 18 males) was also implanted with a bioglogger, called mortality implant transmitters (MITs; Vectronics Aerospace GmbH), which instantaneously notified researchers of death as well as continuously recording body temperature (Herberg et al. 2018, Minicucci et al. 2018). These moose ranged in age from 1 to 16 years old (median=6 years). The collars were programmed to collect the location every 4.25 h, and the MITs were programmed to record body temperature (to the nearest 0.1°C) every 10 or 15 min.

This region has been classified as Northern Superior Upland (Minnesota Department of Natural Resources 2025) and includes bogs, swamps, lakes, and streams; lowland stands of northern white cedar *Thuja occidentalis*, black spruce *Picea mariana*, and tamarack *Larix laricina*; and upland 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 frequently intermixed. Lowland forest types typically offer little in terms of browsing options for moose but rather serve as thermal refuges. This is because mature coniferous wetlands, such as cedar swamps, tend to have canopies with interlocking crowns that limit penetration by sunlight (Minnesota Department of Natural Resources 2025). Deciduous wetland forests also offer thermal refuge in the summer when they are fully leafed out, and canopies are full (McGraw 2019). Black ash and tamarack forests may offer thermal cover but are under threat due to an invasion of emerald ash borer *Agrilus planipennis* and sustained outbreak of eastern larch beetle *Dendroctonus simplex*, respectively (Palik et al. 2021, McKee et al. 2022, Francart 2024). Upland mature hardwood and mixed hardwood–conifer forests, such as those selected by moose, can provide both thermal refugia and browse opportunities as they support a diverse array of tree and shrub species and develop complex canopies and understories that provide thermal relief from light interception by mature canopies and hiding cover from well-developed subcanopies and understory layers. Pine woodlands provide thermal cover and can provide browse when stands mature and begin to develop canopy openings (Minnesota Department of Natural Resources 2025). White-tailed deer *Odocoileus virginianus* overlap with moose throughout the study area, and wolves *Canis lupus* and American black bears *Ursus americanus* serve as the primary predators of both ungulate species (Nelson and Mech 1986, Mech and Fieberg 2014, Severud et al. 2019). Moose hunting has been closed to state-licensed harvest since 2013 due to the population

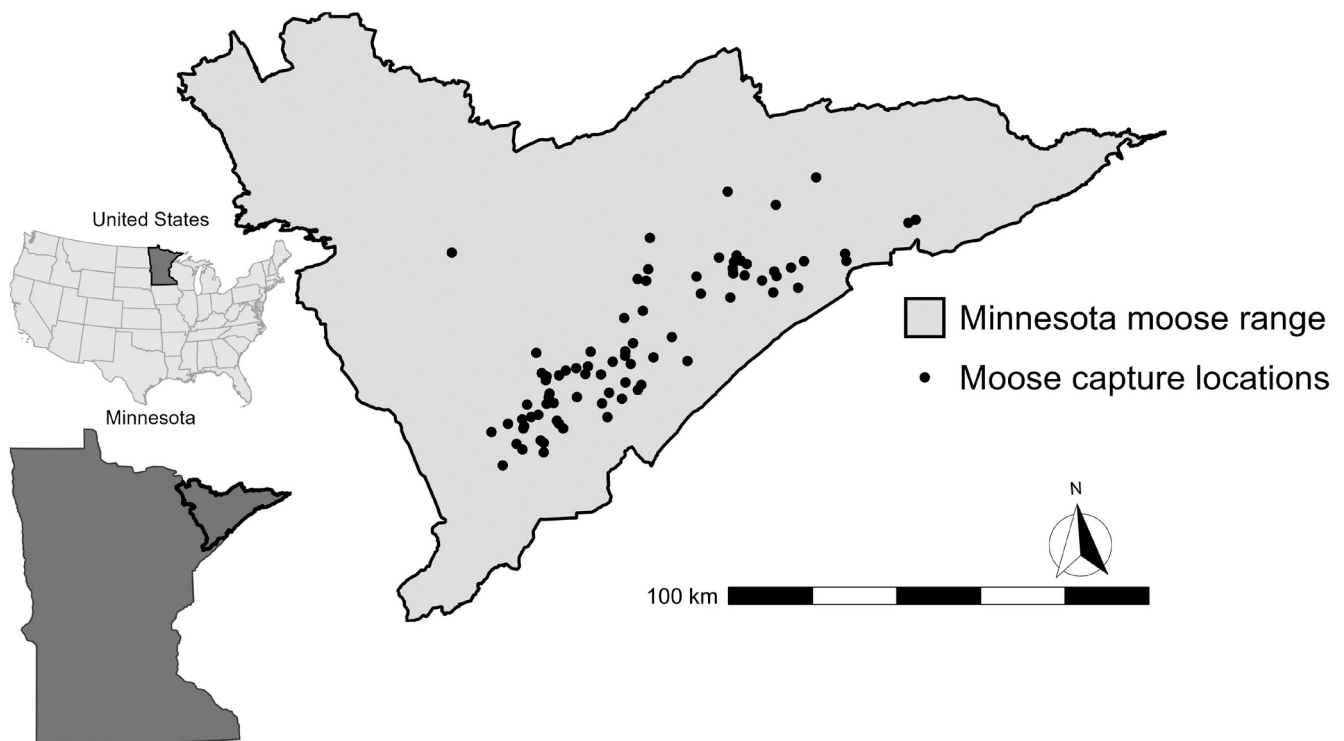


Figure 1. Capture locations of GPS collared moose *Alces alces* fit with mortality implant transmitters for continuous measurement of body temperature (T_b) during 2013–2017 in northeast Minnesota moose range, USA.

decline; however, a limited amount of subsistence and ceremonial harvest (< 50 moose, primarily bulls) by local tribes with retained treaty rights has continued annually. Parasitic infections are a common source of mortality in this moose population, including *Parelaphostrongylus tenius*, liver flukes *Fascioloides magna*, and winter tick *Dermacentor albipictus* (Wünschmann et al. 2015, Carstensen et al. 2017).

We used only summer moose locations for this analysis, given summer was identified as the season most associated with heat stress events for Minnesota moose (Carstensen et al. 2024). Summer dates varied by year, typically starting between 2 June and 7 June and ending between 6 October and 20 October; summer started after parturition and ended when the average temperature fell below freezing (0°C; Carstensen et al. 2024). We censored individuals from the dataset that left the study area, did not have summer locations, or had collar failures. Additionally, location and activity data were excluded one week pre-death from analyses for moose that died during summer to reduce potential effects of acute illness or mortality on moose behavior. All moose that died were immediately investigated for a larger cause-specific mortality study (Carstensen et al. 2017); the timing and cause of death for the subset of animals with MITs used in this analyses was reported in Carstensen et al. (2024). We used the ‘amt’ package (Signer et al. 2019) to generate 95% fixed kernel home ranges (Worton 1989) for every moose–summer combination and generated 10 random points for every used point within those home ranges (Fieberg et al. 2021). From here forward, we refer to ‘moose year’ as one summer of data from an individual moose, like Carstensen et al. (2024). We treated moose years as independent in this analysis because of the interannual differences in weather, age, behavior, and other factors.

Weather variables

Minnesota has a humid continental climate, characterized by hot summers and cold winters. Temperatures as low as −51°C occur during Minnesota winters, while summers as hot as 45°C are also possible (Minnesota Department of Natural Resources 2024). The moderating effect of Lake Superior keeps the northeast region cooler in the summer and warmer in the winter, compared to the rest of the state. We used data from seven weather stations in the study area (ELOM5, FRNM5, KCKC, ISAM5, SEAM5, FBFW, and KTWM) from the US Forest Service’s Remote Automated Weather Station (RAWS) network (Zachariassen et al. 2003). We extracted the most recent air temperature and relative humidity (measured 2 m above ground) reading from the nearest RAWS station (using the minimum Euclidean distance) for every used and random location, similar to our earlier work (Carstensen et al. 2024). We used the ‘weathermetrics’ package in R to calculate the heat index (°C) from relative humidity and temperature for each location to understand how perceived heat load might influence habitat use (Anderson et al. 2013). The heat index is a combination of ambient air temperature and relative humidity (National Weather Service; weather.gov) and is found using the following equation:

$$\text{Heat Index} = -42.379 + (2.04901523 \cdot T) + (10.14333127 \cdot \text{RH}) - (.22475541 \cdot T \cdot \text{RH}) - (.00683783 \cdot T^2) - (.05481717 \cdot \text{RH} \cdot \text{RH}) + (.00122874 \cdot T^2 \cdot \text{RH}) + (.00085282 \cdot T \cdot \text{RH} \cdot \text{RH}) - (.00000199 \cdot T^2 \cdot \text{RH} \cdot \text{RH}),$$

where T = air temperature (F) and RH = relative humidity (%).

Moose body temperature data

We used the same methods and criteria, sensu Carstensen et al. (2024), to characterize when a moose was experiencing body temperatures (T_b) 0.27°C (0.5°F) above the top of the normal range or $\geq 39.17^\circ\text{C}$ as ‘hot’. If a moose had two or more consecutive MIT readings $\geq 39.17^\circ\text{C}$, that event was defined as an HME. To further break down the types of HMEs that occurred, we used mutually exclusive categories to describe the duration and magnitude (acute versus chronic and moderate versus severe) to delineate variation among the HMEs described in Carstensen et al. (2024). In brief, magnitude was categorized as moderate if an HME had a maximum MIT-derived temperature $\geq 39.17^\circ\text{C}$ but $< 39.44^\circ\text{C}$, and severe if the maximum was $\geq 39.44^\circ\text{C}$ (which added 0.54°C [1.0°F] to the high end of the normal range). Duration was categorized as acute, HME < 35 min, or chronic if > 35 min, which was the average HMW duration across the four summers as reported in Carstensen et al. (2024). For the questions we investigate below, we refer to moose experiencing an HME as ‘hot’ (T_{b-H}) and those not experiencing an HME as ‘normal’ (T_{b-N}). Only three of the 41 moose in the study did not have an HME recorded (Carstensen et al. 2024).

Moose activity data

Each GPS collar was equipped with a dual-axis accelerometer that recorded acceleration on horizontal (x-axis) and vertical planes (y-axis) over 5-min intervals (Herberg 2017). Count values on each axis could range from 0 to 255 during each 5-min interval. We used compositional Dirichlet regression (Gueorguieva et al. 2008) to estimate the proportion of time moose spent resting, foraging, and walking/running during each 5-min interval, which predicted moose behavior with high accuracy (RMSE = 0.21; Herberg 2017). Prior observational studies of ungulates documented that most 5-min intervals contain a mix of active and inactive behaviors (Gottardi et al. 2010, Herberg 2017), and these intervals of mixed behaviors can be incorporated using the Dirichlet modeling technique (Herberg 2017). To predict moose behavior during 5-min intervals, we used a training dataset that was validated with direct observations of the behavior of moose at the Moose Research Center (MRC) in Kenai, Alaska (Herberg 2017). The training dataset included 288 5-min intervals from eight individual moose. Captive moose at the MRC were fitted with GPS collars of the same make and model, and with the same dual-axis accelerometers as those deployed on our study moose in northeastern Minnesota.

We built three candidate models with different combinations of accelerometer axes values as fixed effects and chose the most parsimonious model using Akaike’s information criterion (AIC; Burnham and Anderson 2002). We used

Pearson's correlation test to determine if variables included in models were correlated. Our three candidate models were: 1) proportion behavior=x-axis+y-axis counts, 2) proportion behavior=x-axis:y-axis counts, and 3) proportion behavior=($\sum X$ +y-axis counts; Supporting information). Additional movement data, such as step length, were not included as Herberg (2017) found that models were not improved when GPS fixes were > 30 min.

Aligning data streams

To align the separate moose location, HME, activity, and ambient temperature data streams, we used datetime stamps and the 'fuzzyjoin' package in R (Robinson et al. 2018). 'fuzzyjoin' allowed flexible matching criteria when datetime stamps were not exact matches among datasets. For instance, locations were recorded every 4.25 h, whereas MIT temperature values were logged every 10–15 min and activity values were logged every 5 min. Ambient air temperatures were recorded at hourly intervals.

Activity and behavior sensitivity analysis

To determine when we could identify changes in moose behavior related to HMEs, and whether those behavioral changes could be detected at intervals that aligned with GPS fix rates, we assessed activity values and predicted the proportion of time spent active or inactive at several temporal intervals around each HME event for each moose: 30, 60, 120, and 255 min. We started at 30-min intervals because that period would contain a minimum of two MIT temperature recordings (the minimum required to qualify as an HME) and six activity recordings. The remaining intervals were chosen to appropriately scale up and match the 255-min GPS fix interval. For each interval before, during, and after an HME, we calculated the mean activity values from activity loggers and the mean proportion of time spent active or inactive for each type of HME, based on predicted behavior via Dirichlet regression. We visually compared mean activity values with mean proportion of active behavior within each interval to assess when patterns of observed activity and predicted behavior aligned around each HME type. We evaluated differences in activity levels and proportion of time in predicted behaviors, by HME type, using ANOVA and Tukey HSD in R (www.r-project.org).

Identifying moose prone to HMEs

We calculated a weighted number of HMEs per day for each moose during summer by dividing the total number of HMEs each moose year by the number of days the moose was monitored each summer. This approach allowed for direct comparison among individuals by accounting for an unbalanced number of days per individual moose caused by staggered exit of individuals because of mortality or collar malfunction. We defined moose prone to repeated HMEs or 'frequently hot' (FH or T_{b-FH}) as individuals in the 75% quantile of HMEs per day, within each summer. Because of the interannual variation of moose behavior and overall weather among years, it was possible that each moose could be included in > 1 summer.

Moose habitat data

We used the 30-m forest types layer produced by the USDA Forest Service in cooperation with the MN DNR (Donner et al. 2026) to understand moose habitat use. The major cover types were a mix of upland (mature mixed hardwoods, mesic boreal hardwood conifer, mesic northern hardwoods, pine woodland, and young mixed hardwoods), lowlands (acid peatland, ash swamp, black spruce swamp, cedar swamp, and tamarack swamp), wetland, and open water (Supporting information). We used a browse biomass layer to account for food availability in each cell within forest patches in Minnesota's moose range (McGraw et al. 2025). We extracted the total biomass value (kg ha^{-1}) for each used and available point. Based on previous research, HMEs occurred most commonly in the evening hours (Carstensen et al. 2024), so it was important to include day or nighttime as a covariate. We extracted the coordinates and the timestamp for each location and used the 'photobiology' package (Aphalo 2015) in R to delineate daytime and nighttime locations.

Moose resource selection functions

For our 3rd and 4th objectives, we used generalized linear mixed models to understand relationships in moose habitat selection when moose were hot compared to normal body temperatures. We fit generalized logistic mixed models to account for the lack of independence between samples from the repeated measurements on the same moose. We fit these models using the 'lme4' package in R (Bates et al. 2015). For each case (daytime and nighttime datasets), we fit two global models: 1) in the form of habitat use=hot versus not+cover type+interaction between hot versus not and cover type+a year effect with a logit link function and each moose fit as a random intercept, and 2) in the form of an activity-based model wherein use=hot versus not+summer browse+heat index+proportion of time active+interaction between hot versus not and proportion of time active+a year effect with a logit link function and each moose fit as a random intercept. We ran two models for each dataset to avoid over-parameterization while preserving our overall goal to understand how activity and habitat use change as moose get hot. Furthermore, we ran these models on different subsets of data (daytime versus nighttime) because we know moose habitat selection can be inherently different, but we wanted to limit model complexity and the number of interactions. We also explicitly tested if sex and age were important to predicting habitat use, despite previous work on these same data suggesting that these were unimportant in explaining frequency of HMEs or survival (Carstensen et al. 2024). If parameters were unimportant (using an $\alpha=0.05$), we dropped them from the model and refit the models. We set mature mixed hardwoods as the reference habitat type and T_{b-N} moose as the reference moose in the global model. Mature mixed hardwoods account for ~ 47% of the land cover types among locations in the dataset (Supporting information). We scaled the browse and heat index covariates using a standard Z distribution to achieve better model convergence. We added a

weight of 5000 for every random point and a weight of 1 for every used point (Fithian and Hastie 2012, Fieberg et al. 2021). We treated all HMEs the same for this and the following objective because we were interested in the broad differences between moose that were hot (rather than how moose were hot using the HME classifications), and we had an insufficient sample size to fully explore each HME combination when broken out by all the other factors. Note that there is no parameter fit for 2017 for the T_{b-H} moose models because there was only one moose location that contained an HME as we had reached the end of the study; we do however have locations from T_{b-N} moose from before the collars were blown off.

For the 4th objective, we wanted to understand if there were differences in resource selection of moose that were prone to repeated HMEs (T_{b-FH}). We compared differences in resource selection between T_{b-FH} moose and all other T_{b-H} moose during daytime and nighttime. After running all the same models as above on this reduced dataset, we calculated and compared odds ratios (and 95% confidence intervals) to determine which variables were important in describing moose habitat selection and activity level. The reference levels were the same as the previous models, except that T_{b-H} moose were the reference level in this model. The significance of selection or avoidance of landscape variables was determined by whether 95% confidence intervals of the odds ratios included one.

Results

After censoring, 36 moose (16 male, 20 female) contributed HME data over five summers ($n=11$ in 2013, 17 in 2014, 27 in 2015, 17 in 2016, and 7 in 2017; Table 1). The overall average number of locations per moose year was 608 but varied by year because of differences in season dates and the staggered exit of moose.

Behavior prediction

We evaluated 5 503 510 5-min intervals from 36 moose across all years to predict the proportion of time spent in three behaviors: resting, foraging, and walking/running. The best model to predict behavior included one parameter, which was the summed total of x-axis and y-axis activity counts during each 5-min interval (Supporting information). The proportion of time moose were predicted to be active

(i.e. walking/running and foraging) increased with increasing x-axis and y-axis counts, which were highly correlated (Supporting information; Fig. 2). Given the correlation of x-axis and y-axis counts and significant overlap in activity counts between foraging and walking/running (Fig. 2), we lumped these two categories into one behavior that we called ‘active’. Outside of HMEs and the periods immediately around HMEs, moose had lower overall activity values (mean activity = 52, SE = 0.02) and spent an average of 15% (SE = 0.01%) of their time in active behaviors.

However, in the 30 min immediately preceding HMEs, and during HMEs, moose were more active (22%) compared to their ‘normal’ pattern of activity, and spent even more time in active behaviors in the 30 min after an HME (25%, $F_2=296.5$, $p < 0.001$). When we evaluated the amount of time moose spent in active behaviors for 120 min before and after HMEs, moose spent less time in active behaviors before (17%) and after (21%) HME events ($F_2=1243$, $p < 0.001$). Similar to our evaluation of raw activity values, moose spent 22% of their time in active behaviors during HMEs compared to 16% of their time in the 255 min before an HME and 19% in the 255 min after an HME ($F_2=2049$, $p < 0.001$). This finding indicates we were able to detect activity and behavioral changes associated with HMEs at the scale of our GPS location fixes.

Sensitivity analysis

Collectively, moose experienced 5123 HMEs among all summers. The average number of HMEs per summer and per moose was variable across years due to changing sample size of moose in the study each year (Table 1). The average length of an HME was 32 min (range: 5–1065 min; Carstensen et al. 2024). HMEs were categorized by Carstensen et al. (2024) using internal body temperature thresholds (moderate and severe) and temporal duration thresholds (acute and chronic) that resulted in four types of HME: moderate–acute (63%), severe–acute (14%), moderate–chronic (10%), and severe–chronic (13%). While the magnitude and duration of HMEs were important relative to activity levels ($H_3=1681.7$, $p < 0.001$) activity and behavior patterns followed similar patterns before, during, and after HMEs, regardless of type. Because of this, we lumped HMEs into a single category to evaluate differences in resource selection by hot moose versus normal moose.

When we evaluated activity patterns before, during, and after HMEs, we found that moose were most active in the 30

Table 1. Number of moose by season and sex, as well as mean number of locations per moose and mean number of hot moose events (HMEs) per moose, by HME type. The heat index is the ‘apparent temperature’, which is a combination of air temperature and relative humidity and more accurately reflects what the temperature feels like. ¹Heat index calculated using the Rothfusz equation (Anderson et al. 2013).

Year	n		Locations	HMEs	Summer	Heat index (°C) ¹
	Females	Males	Average (range)	Average (range)	n days	Average (range)
2013	8	3	552 (83–726)	32 (1–67)	134	14 (–9 to 36)
2014	9	8	529 (84–670)	66 (1–210)	122	13 (–2 to 37)
2015	15	12	656 (35–711)	95 (1–366)	130	11 (–16 to 37)
2016	8	9	681 (312–784)	62 (1–184)	141	6 (–16 to 39)
2017	3	4	621 (68–748)	1 (–)	134	–2 (–13 to 29)

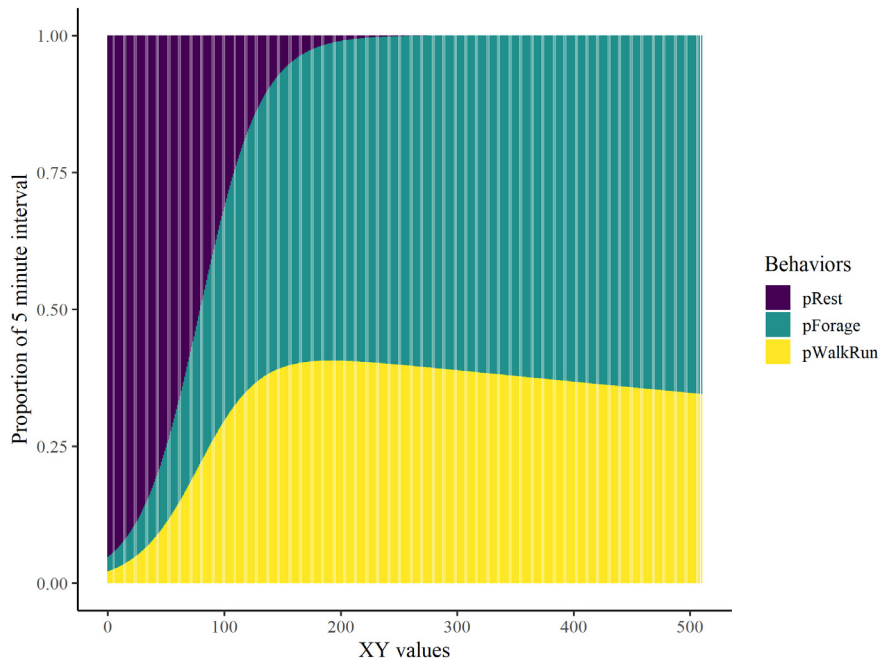


Figure 2. Distribution of predicted behaviors of moose *Alces alces* within 5-min intervals relative to activity values from GPS collar activity loggers deployed in Minnesota (2013–2017). The XY values on the x-axis are the result of a summation of independent x-axis and y-axis activity counts per 5-min interval. The y-axis proportion of each 5-min interval moose spent in different behaviors depending on X and Y values. pRest (purple) is the proportion of time resting, pForage (green) is the proportion of time foraging, and pWalkRun (yellow) is the proportion of time walking and/or running during each 5-min interval.

min leading up to an HME and less active after, regardless of HME type ($F_2=1245$, $p < 0.001$; Supporting information). As we incrementally expanded the time intervals examined around HMEs up to the time between our GPS fix rates (255 min), and therefore averaged across more 5-min activity records, we identified a shift in activity patterns at 120 min before and after HMEs, where moose were more active during HMEs and less active over the 120 min before and after an HME ($F_2=29.24$, $p < 0.001$; Supporting information). The pattern observed at 255 min before and after HMEs was similar in that moose were most active during HMEs and less active in the 255 min before and after an HME ($F_2=428.7$, $p < 0.001$).

When we evaluated the proportion of time spent in active behavior (i.e. foraging and walking/running) in the 30 min before and after HMEs, we saw a different pattern than when we evaluated raw activity values from collar activity loggers. Moose spent similar amounts of time in active behaviors in the 30 min before an HME (22%) and during HMEs (22%) but spent more time in active behaviors in the 30 min after an HME (25%, $F_2=296.5$, $p < 0.001$). However, when we evaluated the amount of time moose spent in active behaviors for 120 min before and after HMEs, we saw a similar pattern to raw activity values, where moose spent less time in active behaviors before (17%) and after (21%) HME events ($F_2=1243$, $p < 0.001$). Similar to our evaluation of raw activity values, moose spent 22% of their time in active behaviors during HMEs compared to 16% of their time in the 255 min before an HME and 19% in the 255 min after an HME

($F_2=2049$, $p < 0.001$). Outside of HMEs and the periods immediately around HMEs, moose had lower overall activity values (mean activity=52, $SE=0.02$) and spent an average of 15% ($SE=0.01\%$) of their time in active behaviors. This finding indicates we were able to detect behavioral changes associated with HMEs at the scale of our GPS location fixes.

Resource selection functions

For all results below, we tested for sex and age differences in each set of the models. In all cases, there were no statistical differences in habitat selection by sex or age ($p > 0.05$). We dropped these terms from the subsequent models and refit the reduced models.

Differences in resource selection between hot moose and normal moose

All habitat selection in our models is relative to mature mixed hardwoods, which in northeast Minnesota is dominated by aspen, makes up $> 40\%$ of the landscape, and is an important habitat type for moose as it can provide abundant forage. During the daytime, hot moose (T_{b-H}) selected habitats differently than normal moose (T_{b-N} ; Fig. 3; Supporting information). After accounting for the other variables in the model, T_{b-N} moose selected fewer land cover types than T_{b-H} moose, overall. Relative to mature mixed hardwoods (i.e. forests typically dominated by aspen), T_{b-N} moose selected for: 1) cedar swamp, mesic northern hardwoods, wetland, and young mixed hardwoods, 2) selected tamarack swamps and mesic boreal conifer in proportion to their availability, and

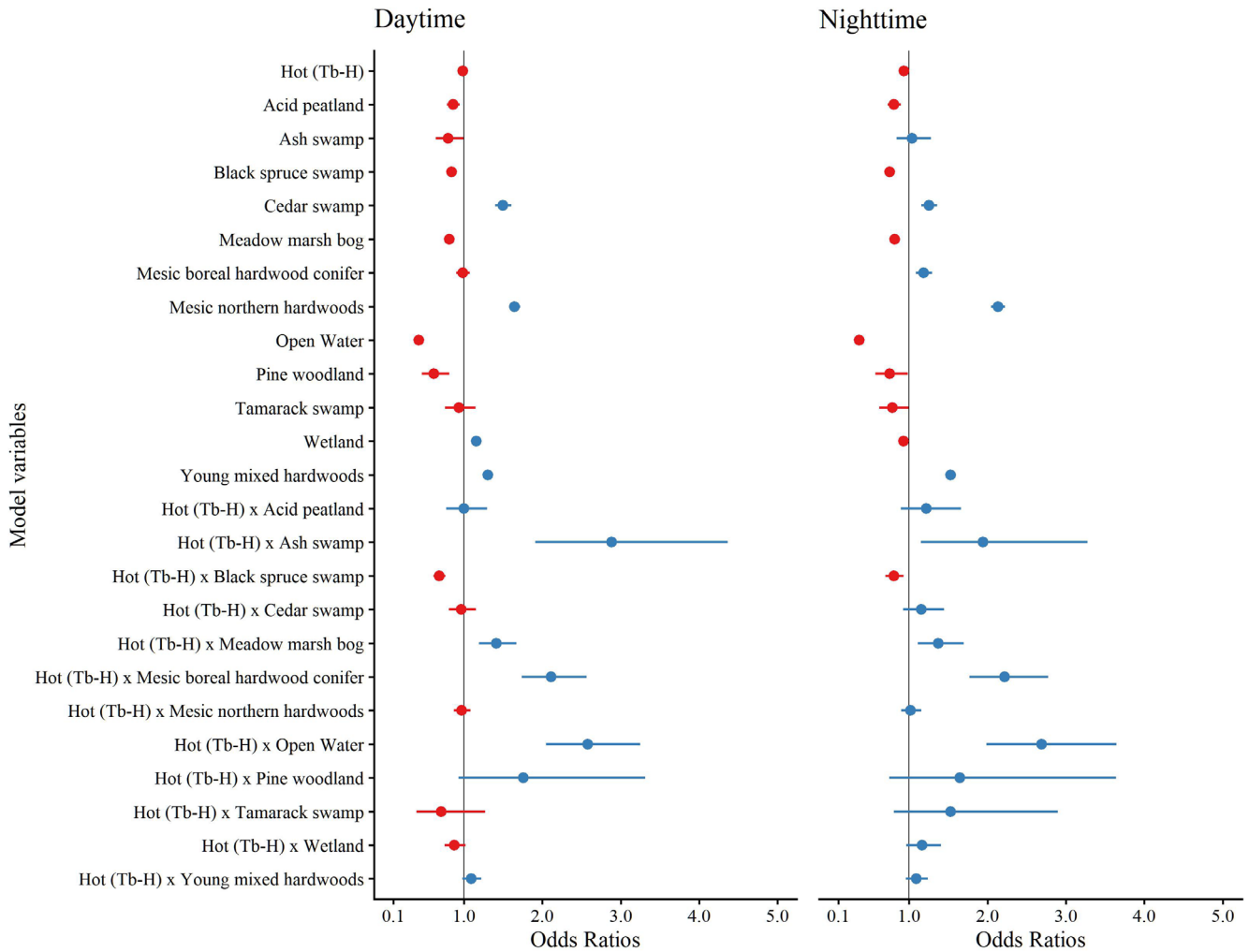


Figure 3. Odds ratios (and 95% confidence intervals) of moose *Alces alces* resource selection functions showing differing patterns of selection from when they were hot (T_{b-H}) or normal (T_{b-N}) between day and nighttime in Minnesota (2013–2017). Mature mixed hardwoods and T_{b-N} are the reference values in the model.

3) avoided all other cover types (Fig. 3). Relative to mature mixed hardwoods and T_{b-N} moose, T_{b-H} moose selected very different habitats: 1) for ash swamps, meadow marsh bog, mesic boreal hardwood conifer, and open water, 2) against black spruce swamp, and 3) used remaining cover types in proportion to availability (Fig. 3). The daytime habitat model explained only a small fraction of the overall variation and all the variation explained in the model was from the fixed effects ($r^2_{\text{marginal}}=0.02$). The random effect explained essentially no dataset variation, and the variance and SD of the moose ID were < 0.0001 for 36 moose IDs among 302 701 locations.

For the daytime activity model, we found that there were differences between T_{b-H} and T_{b-N} moose. On average, T_{b-H} moose were more active overall; the average percent of time active was $\sim 20\%$ higher in T_{b-H} moose (mean = $17.35\% \pm 0.12\%$ CI) than T_{b-N} moose (mean = $14.22\% \pm 0.04\%$ CI) during daytime. The total browse had a positive effect on selection (odds ratio = 1.18; CI: 1.17–1.20) after

accounting for the heat index and the individual year of the study (Supporting information). There was a significant interaction between whether a moose was hot and the proportion of time active ($Z_1 = -4.496$, $p = < 0.001$); as activity increased, both T_{b-H} moose and T_{b-N} moose probability of use declined, but at differing rates (Supporting information). This model explained considerably more variation in the dataset than the habitat model, but again, almost all of the variation explained in the model was from the fixed effects ($r^2_{\text{marginal}} = 0.23$, $r^2_{\text{conditional}} = 0.24$). The variance of moose ID was 0.07 (SD = 0.26) for 36 moose IDs.

At night, hot moose (T_{b-H}) and normal moose (T_{b-N}) also selected habitats differently from each other, but each group used most of the same habitats as they did during the daytime (Fig. 3; Supporting information). The main differences we found were that T_{b-N} moose used fewer habitats at night than during the day; they avoided wetlands and selected for mesic boreal hardwood conifer at night. Relative to T_{b-N} moose, T_{b-H} moose went from avoiding wetlands to using

them in proportion to availability. The nighttime habitat model explained essentially the same amount of variation as the daytime model, and all the variation explained was from the fixed effects ($r^2_{\text{marginal}} = 0.02$). The random effect explained 1% of the dataset variation, and the variance and SD of the moose ID was < 0.001 for 36 moose IDs.

For nighttime activity, there were the same differences among the factors as during the daytime, but the sign of the odds ratio flipped to a positive effect on selection. As during the day, the average percent of time active for T_{b-H} moose was ~ higher (mean = $19.45 \pm 0.18\%$ CI) than T_{b-N} moose (mean = $16.27 \pm 0.04\%$ CI), but both groups were more than 11–13% active at night than during the day. There was a significant interaction between whether a moose was hot and the proportion of time active ($Z_1 = -0.82$, $p < 0.001$); as activity levels increased at nighttime, the probability of use increased for T_{b-N} moose and decreased for T_{b-H} moose (e.g. T_{b-N} moose selected foraging habitats during nocturnal hours, likely for feeding), after accounting for the other variables in the model (Supporting information). The nighttime activity model explained about a third of the overall variation, but nearly all the variation explained in the model was from the fixed effects ($r^2_{\text{marginal}} = 0.32$, $r^2_{\text{conditional}} = 0.33$). The random effect explained 1% of the dataset variation, and the variance of the moose ID was 0.04 (SD = 0.20) for 36 moose IDs.

Characteristics of frequently hot moose

Nearly 42% of all moose were categorized as T_{b-FH} moose in at least one summer during our study. The number of T_{b-FH} moose varied among years ($n = 3$ in 2013, 5 in 2014, 7 in 2015, 4 in 2016, and 0 in 2017). The mean number of HMEs for T_{b-FH} moose was 1.32 per day (range: 0.66–1.75), compared to 0.27 (range: 0.16–0.35) per day for T_{b-H} moose. Male moose accounted for over half of T_{b-FH} moose (56%) when compared to the 46% of GPS collared males. There was no discernible spatial pattern in the distribution of frequently hot moose on the landscape (Supporting information). The sample size was not large enough to evaluate whether disease, parasites, or predation contributed differentially to the mortality of frequently hot male moose versus female moose. However, 50% of T_{b-FH} moose died during the study, compared to 34% of all moose with MITs.

Frequently hot moose versus all other hot moose

In both models (daytime and nighttime comparisons between T_{b-H} and T_{b-FH}), numerical routines identified intra-moose variation was very close to 0. During the day, T_{b-FH} and all other T_{b-H} moose had several notable differences in resource selection. Relative to mature mixed woodlands and T_{b-H} moose, T_{b-FH} moose selected for: 1) black spruce swamps, tamarack swamp, and mesic hardwood boreal conifer, 2) avoided ash swamp and pine woodland, and 3) used all other habitats in proportion to their availability when compared to mixed mature hardwoods (Fig. 4; Supporting information). T_{b-H} moose selected for: 1) ash swamps, meadow marsh bog, mesic northern hardwoods, pine woodland, and young mixed hardwoods, 2) avoided black spruce swamps, and

3) used all other habitats in proportion to their availability (Fig. 4; Supporting information).

For the daytime activity model, we found no evidence for an interaction between activity and T_{b-FH} moose ($Z = -0.106$, $p = 0.665$), nor any statistical difference among years (in all cases, $p > 0.100$) so we dropped the terms and refit the model. There was negligible statistical difference in the proportion of time active during the day between T_{b-FH} (mean: 15.0 ± 0.06 95% CI) and all other T_{b-H} moose (mean: 14.5 ± 0.05 95% CI). After accounting for the heat index and browse, as activity increased, so did the probability of selection for both T_{b-FH} and all other T_{b-H} moose during the daytime (Supporting information). The activity model explained 4% of the variation in the dataset, but this was all due to the fixed effects rather than the random effects.

Similar to the daytime model, numerical routines in the nighttime model identified intra-moose variation very close to 0. We found no evidence for an interaction between activity and T_{b-FH} moose ($Z = -0.297$, $p = 0.766$), so we dropped the term and refit the model. The nighttime habitat model explained essentially the same amount of variation as the daytime model and all the explanatory power was in the fixed effects ($r^2_{\text{marginal}} = 0.05$). Despite this, we were able to detect differences between T_{b-FH} and all other T_{b-H} moose. During nighttime, T_{b-H} moose habitat selection was like the cover types they used during the day, but T_{b-FH} used quite different habitats at night than during the day (Fig. 4; Supporting information). Relative to mature mixed woodlands, T_{b-H} moose selected for: 1) ash swamps, mesic northern hardwoods, and pine woodlands, 2) avoided acid peatlands and black spruce swamps, and 3) used all other habitats in proportion to their availability (Fig. 4; Supporting information). T_{b-FH} moose selected for: 1) acid peatlands, black spruce swamp, cedar swamp, mesic hardwood boreal conifer, and young mixed hardwoods, 2) avoided ash swamp and pine woodlands, and 3) used all other habitats in proportion to their availability when compared to mixed mature hardwoods (Fig. 4; Supporting information).

In the nighttime activity model, we found no difference between T_{b-FH} and T_{b-H} moose ($Z = 0.010$, $p = 0.829$; Supporting information). This model explained negligible levels of overall variation and all the explanatory power was in the fixed effects ($r^2_{\text{marginal}} = 0.01$). Like the daytime model, there was negligible statistical difference in the proportion of time active at night between T_{b-FH} (mean: 17.0 ± 0.05 95% CI) and all other T_{b-H} moose (mean: 16.4 ± 0.06 95% CI).

Discussion

The choices Minnesota moose make in habitat selection and activity level directly relate to the probability they are going to experience heat stress in summer. Carstensen et al. (2024) found that moose prone to repeated HMEs were least likely to survive, and our study suggests this impacts males more than females. Further, it appears that moose are indeed making tradeoffs between thermoregulation and foraging throughout

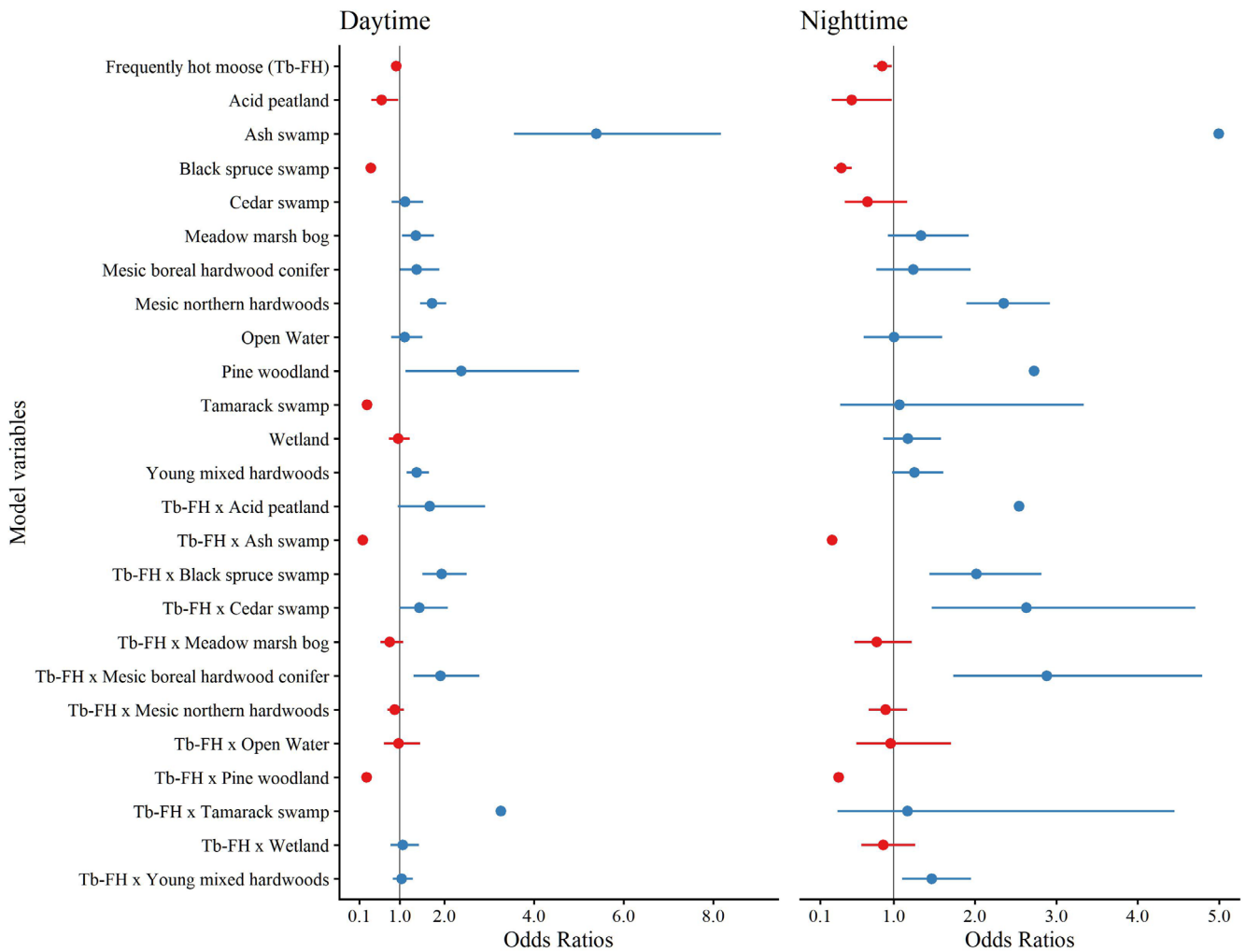


Figure 4. Odds ratios (and 95% confidence intervals) of moose *Alces alces* resource selection functions showing differing patterns in resource selection of moose that were frequently hot moose (T_{b-FH}) compared with all other moose in the study during day and nighttime when hot (T_{b-H}) in Minnesota (2013–2017). Mature mixed hardwoods and T_{b-H} are the reference values in the model.

the day in relation to heat index, and this is impacting their fitness and survival. Numerous past studies have discussed the importance of managing internal and external heat loads as driving feeding ecology in large mammals, and that shifting foraging behavior to cooler times of the day can help maintain thermal homeostasis in hot environments (Hetem et al. 2016, Beale et al. 2018, Borowik et al. 2020). Further, many moose-specific studies have suggested that moose cope with warm summer days by reducing their activity levels, seeking denser canopy cover as the day progresses, and selecting habitats during nocturnal hours likely associated with feeding (Dussault et al. 2004, van Beest et al. 2012, Melin et al. 2014, Street et al. 2015, Ditmer et al. 2018, Montgomery et al. 2019, van der Vegt 2025, Widén et al. 2025). These studies and their reported moose behaviors, although lacking T_b data and being purely observational, align well with what we observed for T_{b-N} moose but fail to explain the behavioral response of T_{b-H} moose. Other studies report a lack of behavioral response of moose to high ambient temperatures in

summer. Lowe et al. (2010) observed no difference in habitat selection of Ontario moose related to increased ambient temperature. Thompson et al. (2021) did not find Alaskan moose selecting different microclimates for rest during hot days, but instead used elevated resting sites in dense canopy, demonstrating moose make choices on the landscape that influence their ability to thermoregulate. Given that our study was the first to pair physiological and behavioral data of wild moose over 5 years with heat indices and habitat selection, our findings suggested that not all moose were making ‘good choices’ in hot environments.

We found that moose were most active in the 30 min preceding an HME and became less active afterward when summarizing the raw activity data. This pattern was consistent, regardless of the type of HME, but the highest activity counts occurred preceding acute–severe events. While we cannot know with certainty the circumstances that led to these rapid increases in T_b for these moose, it is plausible that wolf encounters and predator chases preceded some of these

extreme HME events. Græsli et al. (2020) reported increased resting and marked increases in T_b of moose the day after being chased by hunting dogs in Sweden, with the highest recorded reading of 40.8°C (which is slightly lower than our maximum observed T_b of 41.5°C). Gray wolves are the primary predator of moose in northeast Minnesota and account for approximately a third of all adult moose deaths annually (Carstensen et al. 2017), including 29% of the moose in this study (Carstensen et al. 2024). Given that moose are known to be defensive mothers, predator encounters in summer months may result in fight or flight responses for cows with calves at heel; either behavior could cause an acute-severe HME. Koetke et al. (2025) found that cows with calves in British Columbia were prioritizing habitat selection for vertical cover to reduce risk of direct mortality by predators over the need to avoid heat stress, presuming the landscape offered other strategies to thermoregulate. Yet, without any physiologic data to suggest these moose in British Columbia were ever hot, presuming they were facing a trade-off between predation risk and heat stress is purely speculative. Whereas for Minnesota moose, summer heat stress is documented, and the consequences of the decisions hot moose appear to make are reducing their fitness and survival.

When we modeled moose behaviors at 30 min preceding HMEs using Dirichlet regression, we found opposite activity patterns from the raw data analysis. This result is likely explained as a temporal scale issue, given T_b readings were recorded at 10–15 min intervals and activity at 5 min. The model converged to match the raw activity data at 120 min and held consistently through the 4-h window, when locational fixes occurred. Yet, when averaged over the longer time interval, important behaviors that caused acute T_b increases are missed. Further, the dataset used to train the model was derived from captive moose in Alaska that lacked bouts of high activity (e.g. predator chases) during the observational periods, nor ever experienced heat stress events (Herberg 2018, Thompson et al. 2020). Conversely in our study, 38 of 41 moose experienced HMEs (Carstensen et al. 2024). Thus, it is probable that extrapolating this model to predict wild moose behaviors in natural settings is biased toward reduced activity levels. Further, Herberg (2017) recommended the inclusion of step-length from locational data at fixed rates of 30 min or less to improve the behavioral state predictions; our 4-h fix rates were too temporally coarse to be included in the model. Despite needing to summarize and evaluate raw activity and modeled behavior over 4-h periods around HMEs to align with GPS fix rates on collars, which dampened the signal, we were still able to detect statistical differences in activity and modeled behavior when compared to periods without an associated HME. Moose had higher activity levels and spent more time in active behaviors in the 4-h immediately preceding and after HMEs compared to moose not experiencing HMEs overall. In short, hot moose were more active than normal moose.

What is perplexing is the lack of observed habitat selection response by hot moose between day and night during the same time periods and study area where we were observing

normal moose. Hot moose seemed to be selecting habitats (and often more mesic sites) that were avoided by normal moose (such as meadow marsh bog, mesic boreal hardwood conifer, open water, and wetland). Many habitat types selected by hot moose could provide thermal relief through convective heat loss (bogs, open water, and other wetlands) during day or night, or through shade by canopy cover during the day (mesic boreal hardwood conifer). The lack of selection for young mixed hardwoods, which are generally dominated by regenerating aspen, birch, and maples, by hot moose, regardless of day or night, is also unexpected. This lack of selection could indicate that these moose were making a tradeoff by using foraging habitats less, potentially seeking more thermal relief. This is consistent with moose in Norway that appeared to make a tradeoff between thermal shelter and foraging during summer and exposure to high temperatures, which may have limited forage availability and adversely impacted body condition (van Beest et al. 2012, van Beest and Milner 2013). However, those authors did not have the ability to directly monitor T_b for these moose while observing temperature-dependent behaviors, whereas our ability to deploy biologgers allowed the pairing of physiological and fate data to suggest that tradeoff can be dire.

Conversely, our normal moose exhibited habitat selection and activity patterns more aligned with a tradeoff that favored balancing the need for forage intake and thermoregulation. They increased nocturnal activity and used habitat types that typically provide more forage opportunity and less canopy cover, which would allow for more radiant heat loss (e.g. young mixed hardwoods and mesic northern hardwoods). During the day, normal moose selected for habitats that offer both foraging opportunities as well as thermal refugia (e.g. mesic northern hardwoods, young mixed hardwoods, cedar swamp, wetlands). Similar shifts in behavior and habitat selection relative to ambient temperature have been documented in Norway and Sweden (van Beest et al. 2012, van der Vegt 2025, Widén et al. 2025). This may be a more adaptive strategy that allows moose to persist in increasingly warmer climates.

We found that not all hot moose were the same. We found no difference in resource use between male and female moose, but when we investigated the subset of T_{b-H} moose, they were over half male, were experiencing 5× the daily rate of HMEs, and reduced survival compared to T_{b-H} moose. Sex-based differences in habitat selection were reported for Alaskan moose, where females had a stronger selection for dense canopy as temperatures increased during summer (Jennewein et al. 2020), potentially to avoid expending energy to thermoregulate using physiological mechanisms, given the high caloric demands for nursing. Similarly, male moose in Wyoming had a weaker selection for thermal refuge in summer than females, despite being more likely to overheat (Levine et al. 2025). Males, void of the added demands of calf rearing, may just opt to continue feeding despite increased heat loads, given the high caloric needs to maintain their larger body size while simultaneously expending energy to dissipate heat through increased

respiration and metabolic rates associated with rising ambient temperatures in summer (Renecker and Hudson 1986, 1992). Further, larger-bodied males may likely have more of a challenge to dissipate heat due to their volume:surface ratio being less advantageous than for the smaller-bodied females (Porter and Kearney 2009). The lack of differences between male and female moose in our study could be an artifact of a small sample size (36 individuals in the sample), all of which were suffering from heat stress (Carstensen et al. 2024).

Moose that were frequently heat stressed (T_{b-FH}) used different habitats relative to other hot (T_{b-H}) moose. T_{b-H} moose selected for a mix of foraging cover types (mixed northern hardwoods and young mixed hardwoods) and some thermal cover (ash swamps, pine woodland). However, T_{b-FH} moose selected for less diversity in foraging cover (mesic boreal hardwood conifer) and different thermal cover (black spruce swamp) relative to T_{b-H} moose. All T_{b-H} moose selected ash swamp and avoided black spruce swamp, whereas relative to T_{b-H} moose, T_{b-FH} moose avoided ash swamp and selected for acid peatlands and black spruce swamp.

The selection for black spruce swamp and acid peatlands by T_{b-FH} moose is perplexing because these forest types offer little in terms of food or shelter. This selection for these cover types was in relation to the reference cover type, mature mixed woodlands, which contained a variety of aspen and birch. In Minnesota, acid peatlands can be either wet and treeless or dry and sparsely wooded (Minnesota Department of Natural Resources 2025). Within our study area, the acid peatlands are predominantly in the northern spruce bog subclass (Minnesota Department of Natural Resources 2025), which supports stunted, low-density black spruce *Picea mariana* and the development of thick layers of sphagnum moss. Black spruce swamps consist of forests inundated with water that also foster deep layers of sphagnum moss. Black spruce offer some, albeit weak, thermal shelter from solar radiation, but much less than many other habitat types in the study area. T_{b-FH} moose may seek out black spruce swamps and acid peatlands for thermal refuge when inundated with water, but because these habitats generally rely on precipitation for water inputs, rather than inputs from groundwater sources, this would suggest they act more as ephemeral and unreliable areas of thermal refuge. A changing climate with increasingly drier summers in this region will further limit water inputs to these vulnerable systems (Handler et al. 2014).

Our ability to discern choices in habitat selection made by hot moose was limited by the 4-h fix interval, which was sufficient to inform the broader study goal of determining survival rates and cause-specific mortality, yet was too coarse to explain fine-scale behaviors associated with thermoregulation. Alston et al. (2020) used a 20-min interval and step-selection functions to model Minnesota moose behaviors in summer associated with ambient temperature, and found that moose reduce movements and use shade far more than water to mitigate heat during hot weather, avoiding open water and marsh and selecting for woody bogs and mixed forest as temperature increases. Their behavioral observations supported that moose were making a steep tradeoff during periods of

high heat by selecting for shade and shorter step length as temperatures increased, foregoing foraging in favor of bedding under shade. Further, these authors reported moose selected for shorter distances to mixed forest when it was hot, a concept further supported by Johnson and Rea (2024), who stressed the importance of distance to edge for moose and their requirement for spatially adjacent patches of younger plant communities for forage and older forest for thermal and security cover. Yet when Alston et al. (2020) refined their fix intervals from 20 min to 1, 2, and 4 h, they found far less biologically meaningful relationships between temperature and movement rates, which likely translates to our challenge of discerning key differences in how hot moose were selecting habitats in relation to availability as they appeared to broadly use the landscape. This pattern of selection likely over-simplifies the choices hot moose were making, as thermal variability exists at fine scale across our study area due to the mosaic of vegetation cover types, canopy closure, and site aspect. Olson et al. (2014) reported differences in mean operative temperatures of $\leq 9^{\circ}\text{C}$ across all habitat types during the warmest part of summer used by moose in Voyageurs National Park, a similar landscape to our study area, with slope and aspect accounting for a significant portion of the variation. Thus, small differences in the thermal microclimate may be relevant for moose to thermoregulate, but our coarse fix rate prevents the ability to discern specific landscape features (e.g. slope, aspect, distance to edge or water) that correspond to HMEs and may explain why hot moose appear unable or incapable of mitigating heat stress.

Moose health, including nutritional condition, parasite load, age, and other factors, may play an important role in predisposing some individuals to repeated heat stress, regardless of sex. A case in point is Moose 192, a 12-year-old female that was attacked by wolves during parturition and managed to survive the initial attack but succumbed to her severe injuries several hours later and was found floating in a watery ditch (M. Carstensen unpubl.). Upon necropsy, it was noted that she also had severe liver damage caused by a marked liver fluke infection, was anemic with severe hair loss from a heavy winter tick load, and had healed migration tracts in her brain from a previous *P. tenius* infection. Despite these chronic health challenges, she had achieved a sufficient nutritional plane to ovulate, breed, and even carry a calf to term. We cannot dismiss the complexity of immeasurable challenges these moose face as they make daily behavioral choices to balance caloric and thermal needs while maintaining vigilance from threats they may sense (e.g. predators, humans) and those likely unnoticed (e.g. questing winter ticks in late summer, gastropods containing parasitic larvae on forage). Thus, health status may be as important as the juxtaposition of thermal and forage cover types in explaining the behavioral choices of T_{b-H} moose. Murray et al. (2006) theorized that a direct link may exist between summer heat stress and body condition deterioration of moose in northwestern Minnesota, leading to immunosuppression, reduced reproductive productivity, and higher mortality rates. These moose were exposed to severe liver fluke loads and malnutrition,

likely influencing their susceptibility to heat stress which may have either directly or indirectly increased their risk of death. Moose in northeast Minnesota have similar challenges with parasitism (liver flukes, *P. tenius*, and winter ticks), but habitat quality is higher, and malnutrition is rarely observed. In a recent review paper that spanned moose range across North American and Eurasia, Felton et al. (2024) found that warmer summers consistently showed negative associations with body condition for deer species of all body sizes, but there can be marked individual variation in moose to buffer heat stress. Moose living on the southern end of their range in Norway demonstrated behavioral responses to temperature and seasonal mass change that may be contributing to declines in population performance, albeit the mechanisms that underlie the temperature-mediated habitat–fitness relationship remain poorly understood (van Beest and Milner 2013). Challenges remain to our ability to determine the exact role summer heat stress contributes to both proximate and ultimate drivers of moose mortality.

Conclusions

Carstensen et al. (2024) found that moose in Minnesota are experiencing heat stress during summers, and survival was adversely impacted. Yet, they offered no insights into the behaviors of these moose that may explain why overall fitness was compromised. Here, we paired both activity and habitat selection with HMEs and found that moose experiencing heat stress are not making the same choices as moose that are able to maintain T_b with increasing summer temperatures. Hot moose failed to adopt the behavioral switch to nocturnal foraging habitat made by T_{b-N} , which might improve their overall fitness and survival. Simply put, hot moose appear to make ‘bad choices’ in terms of habitat selection relative to their ability to thermoregulate in summer, which may be lowering their survival. While we were unable to determine key differences in overall landscape composition utilized by both hot and normal moose, it is likely that fine-scale difference in features such as patch size and distance to cover, as well as forest structure like closure of canopy, existence of mid-canopy, and developed shrub layers are key determinants to the choices these moose are making (Melin et al. 2014, Borowik et al. 2020, Johnson and Rea 2024, Stenbacka et al. 2025, Widén et al. 2025). Furthermore, incorporating moose health-related information with the fine-scale habitat characteristics would likely allow for better explanation of the overall variation in habitat use between T_{b-H} and T_{b-FH} moose. Future research should attempt to quantify this difference with fine-scale habitat data in combination with location and health data that can more aptly match body temperature fluctuations of moose during summer. While Minnesota moose represent a species living on the southern edge of their traditional range, it is likely that heat stress is impacting moose elsewhere in North America and Eurasia where climate change impacts combine with other stressors to challenge their fitness (van Beest and Milner 2013). Yet without body

temperature data to assess physiological responses to ambient temperature, heat stress is likely occurring but undiagnosed.

Several of Minnesota’s wetland forests, such as cedar swamps, black ash, and tamarack swamps, are vital sources of thermal shelter but are under varying degrees of threat with changing climate (e.g. acid peatlands; Handler et al. 2014), invasive and native pests (e.g. black ash and tamarack; Kolka et al. 2018, Palik et al. 2021, Francart 2024), and, in some cases, unsustainable extraction (e.g. cedar harvesting without reserves). Because moose in Minnesota are heat-stressed in summers, which is likely contributing to increased mortality and lack of population growth, long-term population health may be improved by creating and maintaining thermal cover habitats rather than maximizing browse biomass. Elmore et al. (2017) concluded that forest management rarely considers thermal cover explicitly or in a spatiotemporally dynamic way, and the lack of this consideration is a major shortcoming of conservation planning. These authors further advocate that restoration and management efforts should specifically consider thermal refuge and identify ‘pinch points’, where thermal conditions experienced by an organism deviate to extreme values that can limit vital rates. Our findings identified this pinch point as hot summer days for moose living in northeastern Minnesota. Future forest management efforts would benefit from supporting both thermal and forage needs of moose to mitigate summer heat stress in populations threatened by climate change.

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Conflict of interest – The authors declare no conflict of interest.

Author contributions

Michelle Carstensen: Conceptualization (lead); Data curation (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Amanda McGraw:** Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Andrew Tri:** Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal);

Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Deahn Donner**: Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Software (supporting); Validation (supporting); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01667>.

Data availability statement

Due to Minnesota state law, ethical considerations, and potential impacts on sensitive wildlife populations, access to the primary GPS tracking data is restricted. These data are available for research purposes upon request from the corresponding author, subject to a data use agreement with the Minnesota Department of Natural Resources. All other code, data, and information can be found in the Zenodo digital repository: <https://doi.org/10.5281/zenodo.20847565> (Carstensen et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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