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ARTICLE

Warm-season heat stress in moose (*Alces alces*)

N.P. McCann, R.A. Moen, and T.R. Harris

Abstract: Understanding how moose (*Alces alces* (L., 1758)) are affected by temperature is critical for determining why populations have recently declined at the southern extent of their North American range. Warm-season heat-stress thresholds of 14 and 20 °C are commonly used to study moose, but the variable response of free-ranging moose to temperatures above these thresholds suggests that moose may be more tolerant to heat. We studied zoo-managed cow and bull moose to identify factors that influence warm-season heat stress. We found clear behavioral and physiological responses to thermal conditions. Moose selected shade, indicating solar radiation affects heat stress. Temperature and wind influenced respiration rates. Heat-stress thresholds for moose occurred at 17 °C when bedded under calm conditions and 24 °C when bedded under wind, demonstrating that the onset of heat stress is sensitive to wind and incorporating wind velocity into analyses would improve investigations of heat stress. Moose showing symptoms of gastrointestinal illness selected wind at lower temperatures than healthy moose, suggesting the effects of climate change will be compounded for health-compromised moose. Determining why moose are declining at the southern extent of their range may require understanding how temperature interacts with wind, moose health, and other factors.

Key words: Alces alces, climate change, heat stress, Minnesota, respiration rate, ungulate.

Résumé : La détermination des causes du déclin récent des populations d'orignaux (*Alces alces* (L., 1758)) dans la partie sud de leur aire de répartition nord-américaine nécessite une compréhension de l'incidence de la température sur ces animaux. Si des seuils de stress thermique durant la saison chaude de 14 et 20 °C sont communément utilisés dans les études sur l'orignal, la réaction variable des orignaux en liberté à des températures plus élevées que ces seuils semble indiquer une plus grande tolérance à la chaleur. Nous avons étudié des orignaux femelles et mâles dans des zoos dans le but de cerner les facteurs qui influencent le stress thermique durant la saison chaude. Nous avons noté des réactions comportementales et physiologiques nettes aux conditions de température. Le fait que les orignaux optaient pour des endroits ombragés indique un effet du rayonnement solaire sur le stress thermique. La température et le vent influençaient les fréquences respiratoires. Les seuils de stress thermique pour les orignaux se trouvaient à 17 °C quand ils étaient couchés dans des conditions calmes, mais à 24 °C quand ils étaient couchés au vent, ce qui démontre que l'apparition de stress thermique dépend du vent et que l'intégration de la vitesse du vent dans les analyses améliorerait les études sur le stress thermique. Les orignaux présentant des symptômes d'affections gastrointestinales optaient pour des endroits venteux à des températures plus faibles que les orignaux en santé, ce qui porte à croire que les changements climatiques auront des effets plus importants sur les animaux dont la santé est compromise. La détermination des causes du déclin des populations d'orignaux dans la partie méridionale de leur aire de répartition pourrait nécessiter une compréhension des interactions de la température avec le vent, la santé des orignaux et d'autres facteurs. [Traduit par la Rédaction]

Mots-clés : Alces alces, changement climatique, stress thermique, Minnesota, fréquence respiratoire, ongulé.

Introduction

Understanding how moose (*Alces alces* (L., 1758)) are affected by temperature is critical for determining how climate change is influencing their populations. Moose are adapted to cold climates and increasing ambient temperatures may create a negative energy balance for moose that inhibits their ability to meet energetic requirements (Murray et al. 2006; Lenarz et al. 2009). A warming climate might increase prevalence of pathogens and the susceptibility of moose to pathogens (Murray et al. 2006; Lenarz et al. 2009). These factors and others could interact or function independently to influence moose populations and contribute to recent population declines at the southern extent of the moose range in North America (Murray et al. 2006, 2012; Lenarz et al. 2010).

Behavioral responses of moose suggest that they are sensitive to heat. During the warm season (late spring, summer, and early fall), moose limit exposure to solar radiation and lower energetic costs associated with being active during high temperatures by reducing daytime travel (Demarchi and Bunnell 1995; Broders et al. 2012), selecting habitats that provide shelter from solar radiation during the daytime (Demarchi and Bunnell 1995; Dussault et al. 2004), and by increasing nighttime activity (Dussault et al. 2004). Thermoregulatory behavior enables moose to reduce heat loads when conditions are thermally stressful.

Physiological responses indicate that moose are intolerant of high temperatures. Moose increase oxygen consumption and respiration rates between 14 and 20 °C during the warm season to reduce heat loads through evaporative cooling (Renecker and Hudson 1986, 1990). These physiological responses are signs of heat stress (Hudson and White 1985) and indicate heat-stress thresholds for moose at 14 and 20 °C (Renecker and Hudson 1986).

The response of free-ranging moose to temperatures above the 14 and 20 °C thresholds has varied. Temperatures above 14 and

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20 °C influenced cover-type selection (Schwab and Pitt 1991; van Beest et al. 2012) and survival (Lenarz et al. 2009) for some moose populations. For other populations, cover-type selection was not influenced by temperatures above 14 and 20 °C (Lowe et al. 2010), moose did not select thermal cover until temperatures reached 24 °C (Broders et al. 2012), and higher calf recruitment occurred when temperatures exceeded 14 and 20 °C during summer (Brown 2011). The variable response of moose to temperatures above 14 and 20 °C suggests that the onset of heat stress for moose occurs at a higher temperature (Lowe et al. 2010; Brown 2011). The 14 and 20 °C heat-stress thresholds were developed from two cow moose (Renecker and Hudson 1986, 1990) and may not be representative of how moose typically respond to temperature (Lowe et al. 2010). Studies of additional moose, including bulls, which incorporate both physiological and behavioral responses to temperature, would improve our understanding of how moose respond to high temperatures.

Factors other than temperature can also influence heat stress. Solar radiation (Bourke 2003; Eigenberg et al. 2005) and wind (Berman et al. 1985; Mader et al. 2010) influence heat stress in ungulates, including moose (Renecker and Hudson 1990). Animals infected with pathogens can have elevated body temperatures (Durando et al. 1994), which may make them more susceptible to heat stress. Larger bodied animals exchange heat at a slower rate than smaller bodied animals due to a lower surface area to volume ratio, causing a lagged response to thermal conditions or thermal inertia (Cain et al. 2006). It is important to consider these and other factors that can influence the relationship between temperature and heat stress.

We monitored zoo-managed cow and bull moose to determine the influence of environmental conditions on warm-season heat stress. Using zoo-managed moose allowed us to monitor respiration rates, bed-site selection, and food consumption in a standardized environment while simultaneously monitoring ambient temperature and other factors that we hypothesized would influence heat stress. We hypothesized that solar radiation and temperature would be the primary drivers of warm-season heat stress, but that other factors including animal health and thermal inertia would be influential. We predicted that food consumption would be reduced during high temperatures. Because of the variable responses of free-ranging moose to temperature, we predicted that the onset of warm-season heat stress would occur at an ambient temperature greater than 20 °C.

Materials and methods

Study area

We studied respiration rates and bedding behavior of two adult bull and two nonlactating adult cow moose at the Minnesota Zoological Garden (MZG) in Apple Valley, Minnesota, between 15 May and 15 October 2012. The MZG is located in east-central Minnesota (46°46′N, 93°11′W) where the climate is continental with cold winters and hot summers. During our study, temperatures averaged 21 °C, wind speed averaged 11 km/h, and 39 cm of rain fell during 44 d (National Oceanic and Atmospheric Administration 2013).

We observed moose bedded within one of five 18.4 m × 5.5 m × 2.4 m (length × width × height) stalls with a northwest–southeast orientation. The northwest end of each stall had a 3.8 m × 5.5 m roof and the remainder of each stall was uncovered. Flooring under each roof was a cement slab. A rubber mat or two adjoining dual-chambered livestock waterbeds (Advanced Comfort Technology, Inc., Reedsburg, Wisconsin, USA) were placed on the cement slab under the roof in one corner of each stall. Flooring for the uncovered end of the stall was crushed limestone covered with 6 cm of woodchips. Moose regularly used rubber mats, livestock waterbeds, and woodchip areas for bedding.

Each stall contained an overhead industrial fan (Model 2MA10A; Dayton Electric Manufacturing Company, Niles, Illinois, USA) located under the roof. Fans were turned on by zookeepers each morning when local forecasts predicted daily high temperatures above 18 °C. Fans were angled toward the corner of each stall where the rubber mat or waterbed was located. Bed sites located under running fans received a constant wind of 18.3 km/h (8183 m^3/h; hereafter wind) according to manufacturer specifications. Wind speeds at bed sites that were not located under running fans were calm or nearly calm (hereafter calm) because the stall walls blocked natural wind (N.P. McCann, personal observation).

Each stall contained a livestock mister that was turned on each morning when local forecasts predicted daily high temperatures above 21 °C. Misters were located in open areas of each stall. Moose were exposed to solar radiation when under misters and moose were rarely observed using them (N.P. McCann, personal observation).

One moose occupied each stall and moose were rotated between stalls daily. When moose were absent, zookeepers cleaned stalls, haphazardly covered rubber mats and waterbeds with 0–6 cm of dry straw, provided food of a known mass, and recorded the mass of food not consumed during the previous 24 h after replacing food that was displaced from the feed bowl. Moose were fed a mean of 7.4 kg of commercial pellets daily (SD = 2.2 kg, N = 480; Mazuri® moose maintenance, moose breeder, or herbivore boost; PMI Nutrition International LLC, Brentwood, Missouri, USA). Pellets were supplemented with 0.6 kg (SD = 0.3 kg, N = 480) of willow (genus *Salix* L.), quaking aspen (*Populus tremuloides* Michx.), or cottonwood (*Populus deltoides* W. Bartram ex Marshall) woodchips and leaves on four or five branches collected from MZG grounds that were not weighed.

Zookeepers rated moose fecal pellets when cleaning stalls. Clumped pellets and diarrhea were rated 1 and were considered indications of gastrointestinal illness. Pellets that were not clumped were rated 0 and indicated normal gastrointestinal function and health. Pellets from each moose were screened by MZG veterinary staff multiple times between May and July 2012. Species of the genus *Salmonella* Lignieres, 1900 were detected from pellets of three moose during May and June 2012 and species of the genus *Campylobacter* Sebald and Véron, 1963 were detected from pellets of one moose during June 2012 (T. Wolf, MZG Associate Veterinarian, unpublished data). Clinical signs of infection such as lethargy and anorexia were not observed even though clumped pellets and diarrhea were observed (T.M. Wolf, MZG Associate Veterinarian, personal communication, 2013). Moose with symptoms of gastrointestinal illness were treated with Probios® Dispersible Powder and Bovine One Oral Gel for Ruminants (Vets Plus, Inc., Menomonie, Wisconsin, USA). Management of moose followed guidelines from the United States Animal Welfare Act (United States Department of Agriculture 2009) and the Association of Zoos and Aquariums (Association of Zoos and Aquariums 2013). Research was approved by the MZG's Animal Management Committee.

Monitoring periods

To acquire data over a range of temperatures, we divided the 0730 to 1630 CST period into three 3 h monitoring periods. Each day we randomly selected one monitoring period and recorded the number of times a bedded moose expanded and contracted its thoracic cavity during two to six 1-min-intervals after a 15 min period without a change in bedded posture elapsed. In addition to respiration rates, we recorded the location of each moose within its stall, bedding materials at the bed site under the roof, and the percentage of each moose that was shaded (in 5% increments). The location of shaded areas within each stall was also recorded. Each stall was considered 100% shaded when conditions were overcast. Ambient temperature and relative humidity were recorded by data loggers (HOBO Model U23-001; Onset® Computer Corporation, Bourne, Massachusetts, USA) every 15 min in two randomly selected stalls. Observations were not made at night due to access restrictions.

Statistical analysis

Selection of shade

We determined if moose bedded in full shade more than 50% of the time when both fully shaded and incompletely shaded bed sites were available to them in their stall by using an exact binomial test (FREQ procedure in SAS® version 9.3; SAS Institute Inc., Cary, North Carolina, USA). Using visual estimates of the percentage of each moose that was shaded, we conservatively categorized moose that were 100% shaded as fully shaded and moose that were less than 100% shaded as incompletely shaded. We used $\alpha = 0.05$ for all significance tests.

Respiration rates

We used linear mixed models (MIXED Procedure in SAS® version 9.3; West et al. 2007) to identify factors that influenced respiration rates for bedded moose. We treated individual moose as random effects and monitoring periods as repeated measures from which we collected multiple observations. We examined variation in respiration rates in response to ambient temperature and dew-point temperature. Dew-point temperature was calculated using ambient temperature and relative humidity data collected in moose stalls (August–Roche–Magnus approximation; Lawrence 2005).

Two-factor models combined ambient temperature and dew-point temperature with each other and with fecal pellet rating, sex, relative humidity, bedding substrate, a binary factor indicating if the stall's mister was running during the observation, and a binary factor indicating if the moose was bedded under wind during the observation. Thermal inertia was investigated by creating two-factor models that included the factors listed above with a factor describing the number of hours between dawn and the observation and by replacing ambient temperature with the mean ambient temperature during the previous 6, 12, and 24 h. For all analyses, we only included factors within a single model that were not collinear (factors with tolerance >0.40, REG Procedure in SAS® version 9.3).

Akaike's information criterion values adjusted for small sample sizes (AIC_c) were used to rank candidate models. Models with $\Delta AIC_c < 2$ had the best relative fit (Burnham and Anderson 2002) and were evaluated using type 3 F statistics. All two-factor models were assessed by including and omitting two-way interaction terms. Respiration rates were log-transformed to improve normality.

Simple linear regressions (REG Procedure in SAS® version 9.3) were used to determine the correlation between respiration rates and factors that were determined to influence respiration rates using linear mixed models and AIC_c. A coefficient of determination (R^2) was calculated by regressing the mean respiration rate and the mean measurement of a selected factor for each monitoring period after log-transforming respiration rates. We used simple linear regression to calculate a R^2 because a single accepted method for calculating R^2 for mixed models has not been identified (Magee 1990; Kramer 2005; Edwards et al. 2008; Liu et al. 2008; Sun et al. 2010).

Piecewise regressions (Ryan and Porth 2007; NLIN Procedure in SAS® version 9.3) were used to determine the onset of heat stress. Piecewise regression fits multiple linear models to a data set after partitioning the data set into groups. Inflection points occur where the models intersect and identify the point at which respiration rates began increasing.

Selection of wind

Logistic regressions (LOGISTIC Procedure in SAS® version 9.3) were used to determine if factors we measured influenced the likelihood that moose bedded under wind. We examined temperature and thermal inertia (the number of hours between dawn and the observation and the mean ambient temperature during the previous 6, 12, and 24 h) using single-factor models and two-factor models that included relative humidity, dew-point temperature, bedding substrate, fecal pellet rating, and sex. Moose that bedded under wind were scored as a success and moose that bedded under calm conditions were scored as a failure.

We included observations that occurred when fans were running in the stall and shade large enough to shield a moose from direct sunlight was available under wind and under calm conditions. Moose selected between multiple shaded bed sites that differed due to presence or absence of wind under these conditions. We used AIC_c for model selection and evaluated any selected model using a Wald χ^2 test and the area under receiver operating characteristics curves (AUC).

Consumption rates

We used linear regressions (REG Procedure in SAS® version 9.3) to determine if the fraction of commercial pellet mass consumed (arcsine square root transformed to improve normality) was correlated with the mean ambient temperature during the previous 24 h. We conducted analyses for all moose. We then partitioned the data set based on apparent gastrointestinal health. Temperature was scaled to 24 h to match the period during which consumption occurred because moose were fed daily. The consumption data set ended on 31 August 2013 after which bulls greatly reduced food intake due to onset of the rut.

Results

Selection of shade

When given a choice, moose selected fully shaded bed sites over incompletely shaded bed sites (binomial exact test, $P < 0.001$). Visual estimates of the percentage of each moose that was shaded during monitoring periods indicated that moose bedded in 100% shade during 80 of 89 monitoring periods and at least 65% shade during 88 of 89 monitoring periods. Only once did a moose bed in 100% sunlight. On average, moose bedded in 100% shade during 90% (SD = 4.6%, N = 4 moose) of monitoring periods.

Respiration rates

We collected 421 respiration-rate observations from four bedded moose (mean = 87 observations/moose, SD = 15 observations/moose) during 125 monitoring periods (mean = 31 periods/moose, SD = 4 periods/moose). Respiration rates ranged from 7 to 126 breaths/min and averaged 36 breaths/min (SD = 23 breaths/min). Variation in respiration rates was best explained by the linear mixed model that included ambient temperature and whether moose were bedded under wind or were not. All other models, including those containing factors representing thermal inertia, yielded $\Delta AIC_c > 2$ and were not evaluated further. The two-factor model containing temperature and wind best explained changes in respiration rates (temperature: $F_{[1,290]} = 79.01$, $P < 0.0001$; wind: $F_{[1,290]} = 28.68$, $P < 0.0001$; $N = 421$). Temperature positively influenced respiration rates and wind negatively influenced respiration rates ($y = e^{1.15 + 0.09 \times \text{temperature} - 0.41 \times \text{wind}}$). The model containing the interaction term for temperature and wind was not evaluated because its $\Delta AIC_c = 5$ and its interaction term was not significant ($F_{[1,289]} = 0.76$, $P = 0.38$, $N = 421$).

We used simple linear regressions to examine the correlation between respiration rates and temperature while controlling for wind. Respiration rates were positively correlated with ambient temperature for moose bedded under calm conditions ($y = e^{1.85 + 0.08 \times \text{temperature}}$; $F_{[1,48]} = 84.18$, $P < 0.0001$; $N = 50$; $R^2 = 0.64$; Fig. 1) and under wind ($y = e^{0.82 + 0.10 \times \text{temperature}}$; $F_{[1,73]} = 50.81$, $P < 0.0001$; $N = 75$; $R^2 = 0.41$; Fig. 2). Regression slopes were similar for the two models (differed by 0.02), whereas the y intercept was more than two times greater for moose bedded under calm conditions (1.85) than for moose bedded under wind (0.82) indicating

Fig. 1. Respiration rates in relation to temperature for moose (*Alces alces*) bedded under calm wind conditions at the Minnesota Zoological Garden in east-central Minnesota during late spring, summer, and early fall 2012. The inflection point for the piecewise regression indicates the onset of heat stress at 17 °C.

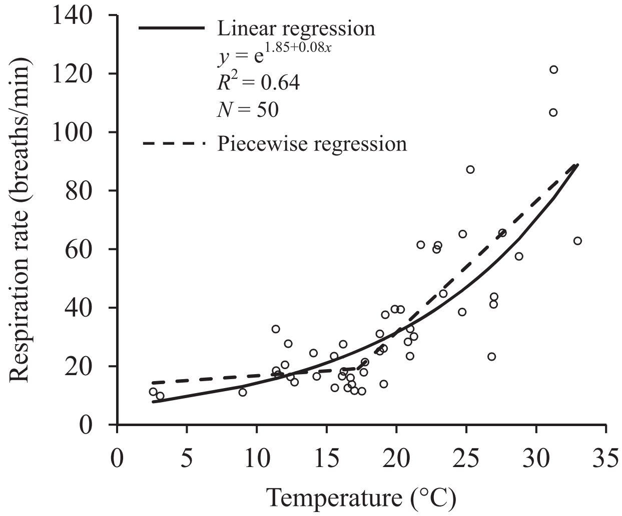
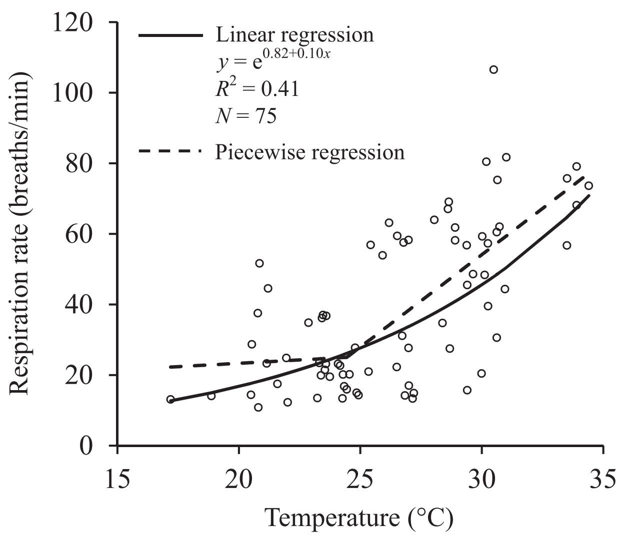


Fig. 2. Respiration rates in relation to temperature for moose (*Alces alces*) bedded under wind at the Minnesota Zoological Garden in east-central Minnesota during late spring, summer, and early fall 2012. The inflection point for the piecewise regression indicates the onset of heat stress at 24 °C.



that higher respiration rates occurred under calm conditions for the range of temperatures that we observed.

Piecewise regression demonstrated the onset of heat stress (increasing respiration rates) at 17 °C (95% CL from 14 to 20 °C) under calm conditions, corresponding to a respiration rate of 19 breaths/min (Fig. 1). Moose increased respiration rates at 24 °C (95% CL from 22 to 27 °C) under wind, corresponding to a respiration rate of 25 breaths/min (Fig. 2). For the range of data that overlapped, respiration rates from least-squares-estimated trend lines were 12–16 breaths/min lower when moose were bedded under wind than when bedded under calm conditions (Figs. 1, 2).

Selection of wind

The likelihood that moose bedded under wind was influenced by the mean temperature over the previous 12 h (hereafter 12 h temperature) and symptoms of gastrointestinal illness (Fig. 3). All other models yielded $\Delta AIC_c > 2$. Of 75 monitoring periods for which shaded bed sites were available in the presence and absence of wind, moose bedded under wind 57 times. The probability of bedding under wind increased with mean 12 h temperature and moose were more likely to bed under wind at lower 12 h temperatures when they had symptoms of gastrointestinal illness (Table 1). AUC for this model indicated good predictive accuracy (Table 1). Models developed from health with temperature measured at the time of the observation and mean temperature from the previous 6 and 24 h were not selected using AIC_c. These models yielded lower AUC scores than the model that included 12 h temperature, but predicted selection of wind well (Table 1).

Moose showing symptoms of gastrointestinal illness were more likely to bed under wind at lower temperatures than moose that appeared healthy (Fig. 3). The probability of moose bedding under wind was 31% higher for moose showing symptoms of gastrointestinal illness when 12 h temperature was 14 °C. When 12 h temperature was 20 °C the probability of bedding under wind was 35% higher for moose showing symptoms of gastrointestinal illness.

Consumption rates

Food consumption was not correlated with temperature for all moose combined ($R^2 = 0.03$; $F_{[1,91]} = 2.36$, $P = 0.13$; $N = 92$) and when data from moose that had symptoms of gastrointestinal illness ($R^2 = 0.08$; $F_{[1,50]} = 3.98$, $P = 0.05$; $N = 51$) or health ($R^2 = 0.00$; $F_{[1,40]} = 0.04$, $P = 0.84$; $N = 41$) were analyzed separately. Moose consumed a mean of 81% (SD = 14%, $N = 92$) of food that they were offered. When calculated separately, moose that had symptoms of gastrointestinal illness consumed 84% (SD = 12%, $N = 51$) of food offered and moose that did not have symptoms consumed 78% (SD = 16%, $N = 41$).

Discussion

We detected clear behavioral and physiological responses by moose to thermal conditions. Moose reduced heat loads by selecting bed sites that were shaded. Solar radiation can cause hyperthermia (Bourke 2003) and is the primary factor causing heat stress in moose (Renecker and Hudson 1990) and other ungulates (Eigenberg et al. 2005). To avoid heat stress during the warm season, moose likely require shelter from solar radiation (Demarchi and Bunnell 1995).

Temperature and wind influenced the onset of physiological heat stress. When bedded under calm conditions, the onset of heat stress for moose occurred at an ambient temperature within the range previously reported (Renecker and Hudson 1986, 1990), which supports a warm-season heat-stress threshold between 14 and 20 °C. The onset of heat stress under wind occurred at a temperature 4–10 °C higher than previously reported, indicating that heat-stress thresholds are sensitive to wind velocity. Wind reduces heat stress through convective and evaporative cooling (Renecker and Hudson 1990; Mader et al. 2006) and may help moose to sustain thermal balance in open environments where temperatures often exceed 20 °C such as in North Dakota's grasslands (Maskey 2008). Incorporating wind velocity into analyses would improve investigations of heat stress in free-ranging moose.

Moose initiated thermoregulatory behavior in response to mean 12 h temperatures by selecting bed sites under wind. Thermal inertia may explain why 12 h temperature was a more accurate predictor of bed-site selection than temperature measured at the time of observations. Moose have low surface area to volume ratios which slows heat transfer and creates a lagged response to thermal conditions. Models developed at other temporal scales were accurate predictors of thermoregulatory behavior but were less accurate than mean 12 h temperature.

Selection of bed sites under wind at lower temperatures indicates that moose with symptoms of compromised health were more susceptible to heat stress than were moose that appeared to

Fig. 3. Probability of moose (*Alces alces*) selecting a bed site under wind at the Minnesota Zoological Garden in east-central Minnesota during late spring, summer, and early fall 2012 in relation to mean temperature during the previous 12 h and apparent gastrointestinal illness and health. Moose showing symptoms of gastrointestinal illness selected wind at lower temperatures than healthy moose. Shaded areas are 95% Wald's χ^2 confidence limits. Data points for successes were offset to improve their clarity by adding 0.01.

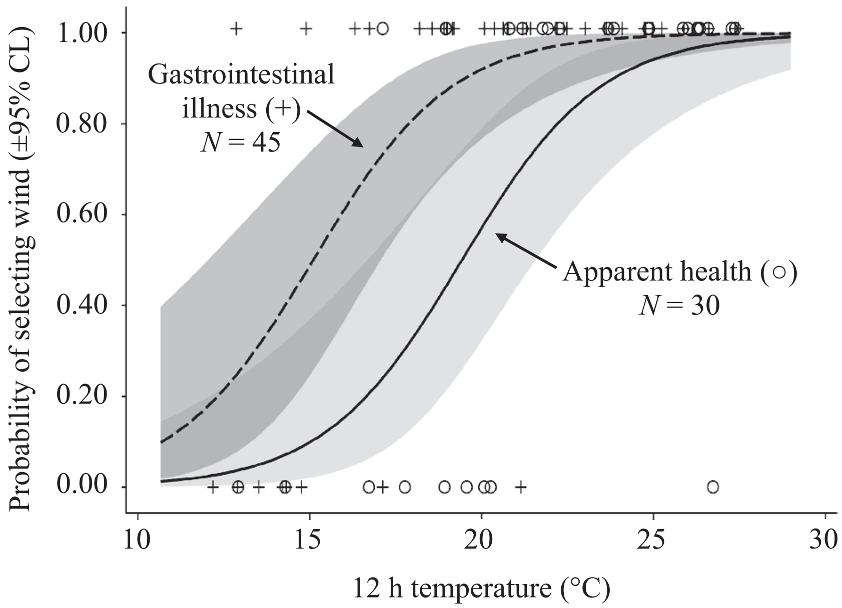


Table 1. Fit statistics and parameter estimates for models predicting the probability that moose (*Alces alces*) bedded under wind at the Minnesota Zoological Garden in east-central Minnesota during late spring, summer, and early fall 2012.

			Temperature			Health		
Model	ΔAIC$_c$	AUC*	Odds ratio (95% CL)	Wald χ^2	*P*	Odds ratio (95% CL)	Wald χ^2	*P*
12 h temperature + health†	0.00	0.89	1.65 (1.29, 2.11)	15.94	<0.0001	0.12 (0.02, 0.61)	6.42	0.01
6 h temperature + health	2.01	0.88	1.49 (1.23, 1.82)	15.74	<0.0001	0.16 (0.03, 0.73)	5.61	0.02
24 h temperature + health	5.39	0.88	1.63 (1.28, 2.08)	15.83	<0.0001	0.13 (0.03, 0.63)	6.45	0.01
Temperature‡ + health	11.11	0.83	1.38 (1.16, 1.63)	13.28	0.0003	0.24 (0.06, 0.91)	4.39	0.04

Note: The selected model included mean temperature during the previous 12 h (12 h temperature) and moose health. Other models that include temperature measured at the time of the observation and mean temperature during the previous 6 and 24 h are shown in descending order based on model fit.

*Area under the resulting receiver operation characteristics curve.

†Model selected using Akaike's information criterion for small sample sizes (AIC$_c$).

‡Temperature measured at the time of the observation.

be healthy. This result has implications for free-ranging moose at the southern extent of their range in North America where a warming climate has been hypothesized to increase risk of infection from pathogens (Murray et al. 2006; Lenarz et al. 2009). Warm-season temperatures are projected to increase at the southern extent of the moose range in North America, including in areas where warm-season temperatures often exceed heat-stress thresholds for moose and have been found to correlate with population declines (Murray et al. 2006; Christensen et al. 2007; Galatowitsch et al. 2009). A warmer climate that increases infection rates for free-ranging moose would compound the effect of higher temperatures because health-compromised moose are more susceptible to heat stress. Additional heat stress could result in diminished biological fitness by reducing the ability of moose to meet energetic demands.

Moose selected bed sites within their stall that allowed them to effectively reduce heat loads when warm-season temperatures were stressful, which has implications for free-ranging moose. Selection of shaded areas by zoo-managed moose is similar to selection of mature forests with high amounts of canopy closure by free-ranging moose during the warm season (Dussault et al. 2004; van Beest et al. 2012). Areas without canopy closure are not selected for daytime use because they lack shade, but could be suitable during the nighttime because solar radiation is absent (Bjørneraas et al. 2011) and radiative cooling is greater in open areas when skies lack cloud cover than within forests (Carlson and Groot 1997). When wind is present, moose would increase convective heat loss by bedding in areas where wind is not impeded by understory vegetation. Shaded areas that lack understory vegetation or which contain sparse understory vegetation should increase heat loss for free-ranging moose on windy days. Openings that contain sparse understory vegetation should increase heat loss on clear, windy nights. Canopy closure and understory vegetation likely combine with thermal conductivity of bedding substrates, browse availability, predation risk, and other factors to influence where free-ranging moose bed during the warm season.

Zoo-managed moose provided an opportunity to study heat stress in a standardized environment with consistent access, which led to more observations of respiration rates and bed site selection than would have been logistically practical to acquire from free-ranging moose. Results from this project are applicable to free-ranging moose, although conditions required for zoo management should be considered. The constant availability of wind at high temperatures may have dampened the response of moose to thermal conditions in our study. Moose could have reduced heat loads by using fan-generated wind, which might explain why food consumption was not reduced at high temperatures in our study. The constant availability of wind could also have raised heat-stress thresholds. On calm days or when wind speeds are low, free-ranging moose would be unable to reduce heat loads like moose under zoo management. Under these conditions heat-stress thresholds would occur at lower temperatures for free-ranging moose.

Solar radiation, wind, and pathogens likely interact with ambient temperature and other factors to influence free-ranging moose populations. In our study, moose nearly always bedded in complete shade during the daytime, indicating that solar radiation is a primary driver of heat stress. Temperature was also a driver of heat stress, but the influence of temperature was reduced by wind and health. Compromised health lowered the tolerance of moose to temperature and is expected to compound the negative effects of a warming climate. Determining why moose are declining in multiple areas at the southern extent of their range may require understanding how temperature interacts with multiple factors that influence heat stress.

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