Body temperature patterns vary with day, season, and body condition of moose (*Alces alces*)

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Variation in core body temperature of mammals is a result of endogenous regulation of heat from metabolism and the environment, which is affected by body size and life history. We studied moose (*Alces alces*) in Alaska to examine the effects of endogenous and exogenous factors on core body temperature at seasonal and daily time scales. We used a modified vaginal implant transmitter to record core body temperature in adult female moose at 5-min intervals for up to 1 year. Core body temperature in moose showed a seasonal fluctuation, with a greater daily mean core body temperature during the summer (38.2°C, 95% *CI* = 38.1–38.3°C) than during the winter (37.7°C, 95% *CI* = 37.6–37.8°C). Daily change in core body temperature was greater in summer (0.92°C, 95% *CI* = 0.87–0.97°C) than in winter (0.58°C, 95% *CI* = 0.53–0.63°C). During winter, core body temperature was lower and more variable as body fat decreased among female moose. Ambient temperature and vapor pressure accounted for a large amount of the residual variation (0.06–0.09°C) in core body temperature after accounting for variation attributed to season and individual. Ambient temperature and solar radiation had the greatest effect on the residual variation (0.17–0.20°C) of daily change in core body temperature. Our study suggests that body temperature of adult female moose is influenced by body reserves within seasons and by environmental conditions within days. When studying northern cervids, the influence of season and body condition on daily patterns of body temperature should be considered when evaluating thermal stress.

Key words: Alaska, *Alces alces*, body temperature, moose, thermoregulation

Endotherms maintain core body temperature through physiological, behavioral, and neuroendocrine responses (Silanikove 2000; Marai and Haeeb 2010; Sejian 2013) to optimize biochemical reactions for metabolism, reproduction, and growth (Prosser and Heath 1991). The amount of energy required for thermoregulation can be influenced by exogenous (e.g., environmental temperature) and endogenous (e.g., heat increment of feeding) factors that can fluctuate on daily and seasonal scales (Silanikove 2000; Barboza et al. 2009; Beale et al. 2017). Homeotherms maintain daily and seasonal core body temperature within a narrow range (IUPS Thermal Commission 2003), whereas heterothermy is a departure from normal homeothermic regulation and may be an adaptation to tolerating fluctuations in environmental temperature or the consequence of insufficient energy to sustain homeothermy (Hetem et al. 2016). The effect of environment on the ability of a large-bodied endotherm to thermoregulate must be distinguished from the normal variation in core body temperature relative to seasonal shifts in metabolism, while considering potential adaptions for heterothermy (i.e., adaptive heterothermy; hyperthermia-induced heterothermy—Cain et al. 2006; Ostrowski and Williams 2006; Hetem et al. 2016).

Seasonal and daily fluctuations in core body temperature have been observed in large-bodied wild and domestic

animals (Fuller et al. 2005; Signer et al. 2011; Turbill et al. 2011; Hetem et al. 2012; Brinkmann et al. 2014). Increased food intake and heart rates during the growing season correspond with increases in core body temperature (Arnold et al. 2004, 2006, 2018; Signer et al. 2011; Brinkmann et al. 2012; Hetem et al. 2016). Diurnal patterns in core body temperature can be affected by exogenous and endogenous factors. For example, Arabian ungulates, during times of high ambient temperature and low water availability, conserve body water by becoming mildly hyperthermic during the day and dissipating the accumulated heat load at night when environmental temperatures are cooler (hyperthermia-induced heterothermy—Ostrowski and Williams 2006; Hetem et al. 2012, 2016). During winter, animals living in temperate climates use nocturnal hypometabolism to decrease energy costs by decreasing peripheral skin temperature and heart rate (Arnold et al. 2004; Brinkmann et al. 2012), whereas alpine ibex (*Capra ibex ibex*) take advantage of solar radiation in the morning to rewarm core body temperature without endogenous heat production associated with increased heart rate (Signer et al. 2011).

Recently, Hetem et al. (2016) hypothesized the possibility of hypothermia-induced heterothermy. During times of low forage availability (i.e., winter in northern climates), animals should have a low core body temperature with high variation in daily core body temperature. Indeed, low body temperatures (Signer et al. 2011; Turbill et al. 2011; Arnold et al. 2018) and high daily variation in core body temperature (Signer et al. 2011; Brinkmann et al. 2014) coincide with seasons of poor forage quality in some animals from cold climates. Furthermore, Hetem et al. (2016) purport that during winter at times of low forage availability, animals in poor condition would have a low daily mean temperature and high daily variation in temperature. Hypothermia-induced heterothermy as a function of body condition has been demonstrated in food-restricted equids (Brinkmann et al. 2014) but has not been studied in wild ungulates living in cold environments. Evaluating continuous measurements of core body temperature from a large-bodied, northern ungulate, can provide insights into the dynamics of homeothermy and heterothermy for these animals.

In northern climates, continuous core body temperatures have been measured on free-ranging pronghorn (*Antilocapra americana*—Lust et al. 2007; Hébert et al. 2008), alpine ibex (Signer et al. 2011), and Svalbard reindeer (*Rangifer tarandus platyrhynchus*—Arnold et al. 2018). For moose (*Alces alces*), records of core body temperature historically have been limited to single measures of moose either under chemical immobilization (Franzmann et al. 1984; Neumann et al. 2011; Evans et al. 2012; Barros et al. 2018) or tethered in stalls (Renecker and Hudson 1986a). Recently, two devices to record continuous core body temperature in free-ranging moose have been validated (Herberg et al. 2018; Thompson et al. 2018). Several studies on moose have evaluated how warming environmental temperatures can negatively influence their fitness (Murray et al. 2006; Lenarz et al. 2009; van Beest and Milner 2013; Monteith et al. 2015; Ruprecht et al. 2016). Only two studies, with small sample sizes and moose confined to small enclosures, have documented an actual physiological response of moose to warm environmental temperatures (Renecker and Hudson 1986a; McCann et al. 2013). Using measurements of continuous body temperature from free-ranging moose could provide a physiological baseline to evaluate when moose are challenged by exogenous and endogenous factors to maintain core body temperature.

We used data loggers in free-ranging female moose to explore temporal fluctuations in core body temperature and to evaluate if endogenous and exogenous factors influence core body temperature, within the context of the hypothermia-induced heterothermy hypothesis (Hetem et al. 2016). First, we predicted that core body temperature of moose would be lowest during winter when food intake, activity, and fasting metabolic rate are at the annual nadir (Schwartz et al. 1984; Regelin et al. 1985; Bevins et al. 1990). Second, we predicted that core body temperature of moose would have the highest daily amplitude during winter. We expected that homeothermy of moose is affected by the added costs of pregnancy and by the available stores of energy in fat. Consequently, we predicted that pregnant moose would have a greater daily amplitude in core body temperature, compared with non-pregnant animals. Last, we predicted that female moose in poor body condition during winter would have lower core body temperature than moose in good body condition because energy use could be repartitioned by relaxing thermoregulatory setpoints. We also examined how exogenous factors associated with environmental temperature (ambient air temperature, relative humidity, solar radiation, precipitation, and wind) influenced daily mean and daily amplitude in core body temperature, and time of day for maximum and minimum core body temperature.

Materials and Methods

All procedures for care, handling, and experimentation of animals followed guidelines of the American Society of Mammalogists (Sikes et al. 2016), and were approved by the Animal Care and Use Committee, Alaska Department of Fish and Game, Division of Wildlife Conservation (protocol no. 09-29, protocol no. 2013-21, and protocol no. 2014-17) and by the Agricultural Animal Care and Use Committee, Texas A&M AgriLife Research (protocol no. 2016-008A).

Animals and climate.—We studied adult (≥ 2 years old) free-ranging captive and wild moose on the northern lowlands (60°36′ N, 150°40′ W) of the western Kenai Peninsula, Alaska, United States, in Alaska Department of Fish and Game - Game Management Units 15A and 15B. Free-ranging captive moose of known age (hereafter referred to as captive; i.e., maintained on natural vegetation in 2.6-km^2 enclosures) were studied at the Alaska Department of Fish and Game Kenai Moose Research Center located within Game Management Unit 15A (60°42′ N, 150°26′ W). Game Management Unit 15A (3,400 km^2) was comprised of mid to late seral state boreal forest due to large wildfires in 1947 and 1969, which burned ~48% of Game Management Unit 15A, resulting in mixed stands of ≥ 45% boreal forest with patches of relic old growth that

is at least 120 years old (Miner 2000). Existing vegetation in Game Management Unit 15B (2,900 km^2) was early seral and old growth boreal forest of which over 800 km^2 was burned in 2014 (Alaska Type 2 Black IMT 2014). The 9.7-km^2 Kenai Moose Research Center had a mixture of early seral boreal forest (1–4 years post mechanical treatment), mid seral boreal forest (25 years post mechanical treatment), old growth boreal forest, black spruce forest, bog, and open meadow. A National Oceanic and Atmospheric Administration (NOAA), U.S. Climate Reference Network weather station (AK Kenai 29 ENE; hereafter referred to as NOAA weather station) was located at the Kenai Moose Research Center (Diamond et al. 2013). The NOAA weather station recorded ambient air temperature (°C), precipitation (mm), wind speed (m/s), solar radiation (W/m^2), and relative humidity (%) every 5 min (Diamond et al. 2013). Relative humidity and ambient air temperature were used to calculate dew point temperature (°C), and dew point temperature was used to calculate actual vapor pressure (hPa—Alduchov and Eskridge 1996).

Animal handling.—We immobilized wild female moose with a mixture of 4.5 mg Carfentanil citrate (0.01 mg/kg estimated body mass; 3 mg/ml; ZooPharm, Windsor, Colorado) and 100 mg Xylazine HCl (0.22 mg/kg estimated body mass; 100 mg/ml; Lloyd Laboratories, Shenandoah, Iowa) administered via a 3-cc dart fired from a rifle (Palmer Cap-Chur, Douglasville, Georgia) in a helicopter (Robinson R-44 [Robinson Helicopter Company, Torrance, California] or Hughes 500 [Bell Helicopter, Fort Worth, Texas]). We reversed wild moose with 400 mg Tolazoline HCl (0.88 mg/kg estimated body mass; 100 mg intravenous, 300 mg intramuscular; 200 mg/ml; ZooPharm) and 450 mg Naltrexone HCl (100 mg/mg Carfentanil; intramuscular; 50 mg/ml; ZooPharm). We immobilized captive female moose by intramuscular hand-injection with a mixture of 0.45 mg Carfentanil citrate (0.001 mg/kg estimated body mass) and 25 mg Xylazine HCl (0.055 mg/kg estimated body mass). We reversed captive moose with 400 mg Tolazoline HCl (0.88 mg/kg estimated body mass; 100 mg intravenous, 300 mg intramuscular) or Atipamezole HCl (0.004–0.005 mg/kg estimated body mass; 2.0–2.5 mg intravenous; 5 mg/ml; Zoetis, Parsippany, New Jersey), and 100 mg Naltrexone HCl (222 mg/mg Carfentanil; intramuscular).

Between 16 November 2014 and 5 December 2017, we collected body temperature for periods ranging from 51 to 360 days from wild and captive female moose. We deployed a vaginal implant transmitter (Model M3970, Advanced Telemetry Systems, Isanti, Minnesota) modified by incorporating a temperature data logger (ARChive ARC400; accuracy 0.5°C, resolution 0.25°C; Advanced Telemetry Systems) which recorded temperature at 5-min intervals (Burfeind et al. 2011; Burdick et al. 2012; Thompson et al. 2018). We inserted cold sterilized (2% chlorhexidine diacetate solution; Nolvasan Solution; Fort Dodge Animal Health, Fort Dodge, Iowa) vaginal implant transmitters into the vagina of immobilized wild (n = 29) and captive (n = 11) moose with a lubricated (OB Lube; Jorgensen Laboratories Inc., Loveland, Colorado), sterilized speculum (Sterile Disposable Vaginal Speculum; Jorgensen Laboratories

Inc.) following the procedures outlined in Patterson et al. (2013). In wild moose, vaginal implant transmitters were either recovered after being expelled at parturition, or if the moose was not pregnant, it was recaptured, and the vaginal implant transmitter was manually removed while the animal was immobilized. In this study, mean parturition date was 21 May as determined by evaluating the data on vaginal implant transmitters expelled from wild moose, with an estimated conception date of 2 October (231-day gestation—Schwartz and Hundertmark 1993). In captive moose, the vaginal implant transmitter was manually removed without immobilizing the animal. We measured maximum rump fat thickness (MAXFAT) via ultrasonography (Ibex Pro, E.I. Medical Imaging, Loveland, Colorado) of each moose under chemical immobilization (Stephenson et al. 1998). We collected blood by jugular venipuncture into a 10.0 ml glass serum tube (BD Vacutainer PN#366430, Becton, Dickinson and Company, Franklin Lakes, New Jersey), which we then spun to separate the serum. We analyzed serum for pregnancy specific protein B (Sasser et al. 1986) to determine reproductive status of each animal.

Calculations and statistics.—We censored vaginal temperature data to remove acute effects of immobilization and parturition. Core body temperature was elevated for 2 days after chemical immobilization; therefore, we excluded all vaginal temperature data for 3 days post-capture. Additionally, core body temperature of pregnant moose increased rapidly before parturition. We excluded data for 9 days before parturition for pregnant animals to account for variation in vaginal temperature between individuals. We used complete 24-h days (midnight to midnight) and excluded any records of partial days. One wild moose was killed by predators and complementary activity and location data from its Global Positioning System collar indicated the moose was chased and killed in the same day; therefore, we removed vaginal temperature records from our analysis for the day of death. Out of 29 vaginal implant transmitters deployed in wild moose, we used 25 for analysis. We removed vaginal temperature data from two wild moose that died shortly (< 5 days) after capture. Furthermore, we removed vaginal temperature data from a young wild moose (age = 4 years) who was not pregnant and whose vaginal implant transmitter recorded data that were similar to biologically infeasible data collected in nulliparous captive female moose (Thompson et al. 2018). Lastly, one vaginal implant transmitter from a wild moose was expelled but never recovered from the field.

We analyzed data using programs in STATA version 15.0 (StataCorp LP, College Station, Texas). We used a robust sandwich estimator for the variance-covariance matrix of estimates for all regression models (Rabe-Hesketh and Skrondal 2010) to minimize the effects of heteroscedacity and non-normal distributions. We used mixed model regressions to evaluate the dependent variables of average daily core body temperature, daily change in core body temperature, and the time of day that minimum and maximum core body temperature occurred. We added individual as a random effect nested within Julian date (D) with an AR1 correlation structure to correct

for autocorrelation (Levesque et al. 2014). Categorical variables included population (captive or wild), reproductive status (pregnant or non-pregnant), and their interaction. We used a spline fit to the continuous variable Julian date (7 knot spline based on percentiles for large sample sizes—Harrell 2001) to test for seasonal variation in the dependent variable. Linear fixed effects were examined with a Wald test, and model explanatory variables were compared with zero using a z-test. We selected the best model for each dependent variable with Akaike's information criterion, adjusted for small sample sizes (AICc), by selecting the simplest model with the lowest AICc within 2 AICc units of the top model (Burnham and Anderson 2002). Number of moose ($n_m = 36$) and number of observations ($n_o = 8,621$) was consistent for all dependent variables. We calculated the daily change in core body temperature as the difference in maximum and minimum daily vaginal temperature for each moose. To determine time of day that minimum and maximum core body temperature occurred, we used the hourly average vaginal temperature for each moose. We then identified the hour of day for minimum and maximum core body temperature for each moose, for every day. We converted the hour into degrees for circular data analysis to determine the daily circular mean for the hour of day that minimum and maximum core body temperature occurred, respectively (Zar 1999; Patterson et al. 2016). We used the daily circular means for time of day of minimum (07:01) and maximum (18:50) core body temperature to center the daily scales for statistical analysis.

After accounting for seasonal variation, reproductive status, population, and individual, we used multiple linear regression

to evaluate if the residuals from each of the selected mixed model regressions for average daily core body temperature, daily change in core body temperature, and the time of day that minimum and maximum core body temperature occurred was influenced by environmental variables. Environmental variables from the NOAA weather station included the daily mean and daily range (maximum minus minimum) of ambient air temperature, vapor pressure, and solar radiation, in addition to the daily total precipitation and mean daily wind speed. We used AICc model selection as outlined above to select the best model for each dependent variable. To determine how each environmental variable in the selected model (Table 1) influenced the dependent variable, we used the regression equation to predict the outcome for the minimum and maximum observed values of each environmental variable, while holding all other environmental variables constant at their respective means.

To evaluate if body condition influenced daily body temperature during winter, we used mixed model regressions of average daily core body temperature, daily change in core body temperature, daily maximum and daily minimum core body temperature from 1 December 2014 through 1 March 2015 for 16 moose (wild $n = 11$; captive $n = 5$). We measured maximum rump fat thickness for each moose both in early (November–December 2014) and late winter (March–April 2015). We assumed a linear relationship of fat loss between the early and late winter MAXFAT measurements (Cook et al. 2001, 2007); therefore, we estimated daily MAXFAT for each individual and used this as a covariate for the time between actual MAXFAT measurements. We converted maximum rump fat thickness to

Table 1.—Parameter estimates, associated *SE*, *t*-value, and *P*-value from the selected linear regression models of residuals of core body temperature of moose (*Alces alces*) parameters against a suite of environmental variables (Supporting Information SD4–SD7). Daily average core body temperature, daily change in core body temperature, and time of day of maximum and minimum core body temperature recorded in free-ranging captive and wild moose on the Kenai Peninsula, Alaska from November 2014 through December 2017. Number of moose $n_m = 36$; number of observations $n_o = 8,621$. Δ = daily range; Σ = daily total; $\bar{x}$ = daily mean.

Response variable	Model variable	Estimate	SE	*t*-value	*P*-value
Residuals – daily average core body temperature (°C)					
	Intercept	−0.005	0.0095	0.59	0.552
	$\bar{x}$ Ambient temperature (°C)	−0.002	<0.001	−3.93	< 0.001
	Δ Ambient temperature (°C)	−0.003	<0.001	−4.79	< 0.001
	Δ Vapor pressure (hPa)	0.011	0.003	3.57	< 0.001
Residuals – daily change in core body temperature (°C)					
	Intercept	−0.083	0.010	−8.41	< 0.001
	Δ Ambient temperature (°C)	0.008	0.001	9.88	< 0.001
	Σ Precipitation (mm)	−0.003	0.001	−2.30	0.021
	$\bar{x}$ Solar radiation (W/m^2)	0.001	<0.001	6.67	< 0.001
	Δ Solar radiation (W/m^2)	< −0.001	<0.001	−7.42	< 0.001
	$\bar{x}$ Wind speed (m/s)	0.017	0.005	3.39	0.001
Residuals – time of day of maximum core body temperature (h)					
	Intercept	−0.972	0.273	−3.55	< 0.001
	$\bar{x}$ Ambient temperature (°C)	−0.122	0.017	−7.18	< 0.001
	$\bar{x}$ Solar radiation (W/m^2)	0.007	0.001	9.05	0.001
	$\bar{x}$ Vapor pressure (hPa)	0.129	0.037	3.47	0.003
	$\bar{x}$ Wind speed (m/s)	−0.318	0.107	−2.98	< 0.001
Residuals – time of day of minimum core body temperature (h)					
	Intercept	−0.879	0.190	−4.63	< 0.001
	$\bar{x}$ Ambient temperature (°C)	−0.048	0.009	−5.38	< 0.001
	Δ Ambient temperature (°C)	0.092	0.019	4.87	< 0.001
	Σ Precipitation (mm)	−0.064	0.022	−2.86	0.004
	$\bar{x}$ Solar radiation (W/m^2)	0.005	0.001	3.81	< 0.001
	$\bar{x}$ Wind speed (m/s)	−0.500	0.104	−4.81	< 0.001

ingesta-free body fat (IFBFAT; %) prior to analyzing the data (IFBFAT = 5.61 + 2.05 × MAXFAT—Stephenson et al. 1998). Model explanatory variables included IFBFAT, with individual as a random effect incorporating an AR1 correlation structure.

RESULTS

Ambient air temperature increased from an average low of −14.7°C to an average high of 16.4°C, with a maximum temperature of 28.5°C recorded during June and a minimum temperature of −37.3°C during December (Fig. 1A). Likewise, solar radiation peaked at the summer solstice, with a maximum of 1,128 W/m^2 and declined to a low at the winter solstice of 26 W/m^2 (Fig. 1B). Vapor pressure ranged from a high of 18.2 hPa in summer to a minimum of 0.2 hPa in winter (Fig. 1C). Daily average wind speed was highest in the spring (Fig. 1D), while

total daily precipitation was highest in late summer and early autumn (Fig. 1E).

We collected over 2.4 million vaginal temperature measurements at 5-min intervals from 36 female moose, which we then used for analyses of daily core body temperature. Body temperatures ranged from 36.25°C to 41.25°C, with the greatest frequency occurring between 37°C and 39°C (Fig. 2). The best model for daily average core body temperature included the categorical variables for population and reproductive status, but not their interaction (Supplementary Data SD1 and SD2). Statistically, pregnant female moose were warmer than nonpregnant moose (0.18°C; Supplementary Data SD2 and SD3), and captive moose were warmer than wild moose (0.24°C; Supplementary Data SD2 and SD3); however, these differences are within the accuracy of the data logger (0.5°C). Given the low accuracy of the logger and the small differences between
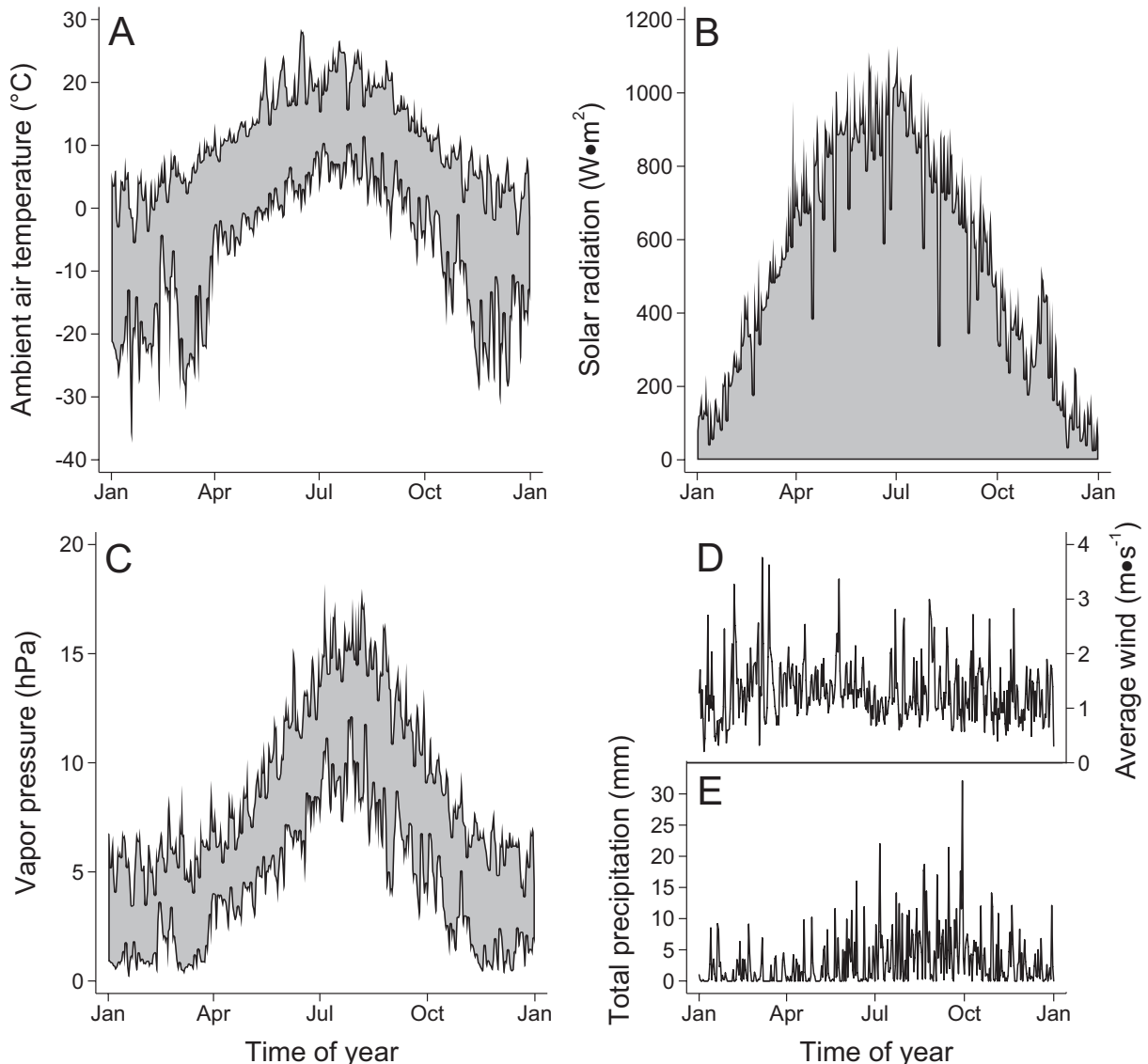

Fig. 1.—A) Range in daily ambient air temperature (°C), B) range in daily solar radiation (W/m^2), C) range in vapor pressure (hPa), D) mean daily wind (m/s), and E) total daily precipitation (mm) recorded from 16 November 2014 to 5 December 2017 by a weather station of the National Oceanic and Atmospheric Administration, U.S. Climate Reference Network (AK Kenai 29 ENE) located at the Kenai Moose Research Center on the Kenai Peninsula, Alaska.
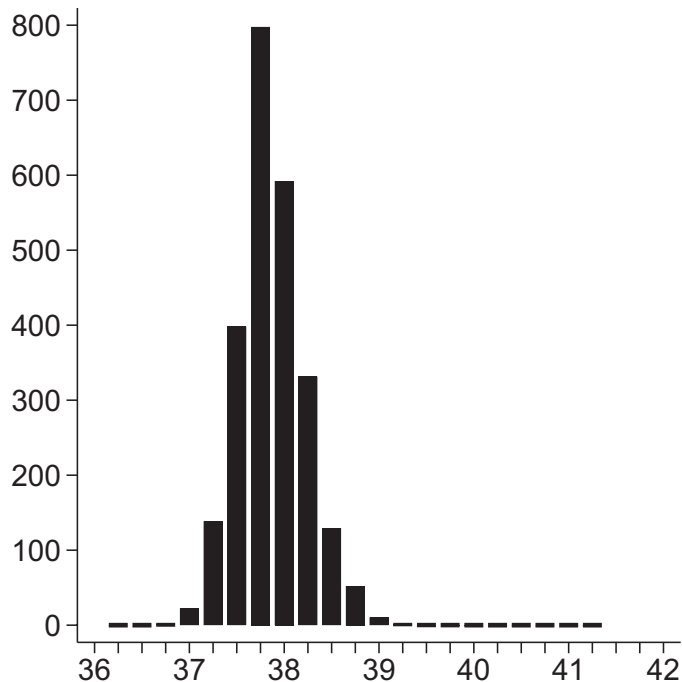
Fig. 2.—Frequency distribution (at 0.25°C intervals) of core body temperature measured with a modified vaginal implant transmitter between 16 November 2014 and 5 December 2017 in free-ranging captive moose (*Alces alces*; *n* = 11) at the Kenai Moose Research Center and wild moose (*n* = 25) on the Kenai Peninsula, Alaska.

the categorical variables for average daily core body temperature, we removed the categorical variables of population and reproductive status from all models (all dependent variables are derived from average daily core body temperature) and only assessed each dependent variable for seasonal variation. Daily average core body temperature exhibited seasonal variation and was highest in summer (38.2°C, 95% *CI* = 38.1–38.3°C) and lowest in winter (37.7°C, 95% *CI* = 37.6–37.8°C; Fig. 3A; Wald χ^2 = 624.71, *P* < 0.001). The best model for assessing whether environmental variables influenced daily average core body temperature included ambient air temperature and the range in both ambient air temperature and vapor pressure (Table 1; Supplementary Data SD4), which accounted for 0.06–0.09°C of the variation in daily average core body temperature over the range of the environmental variables (Table 2).

Daily change in core body temperature also exhibited seasonal variation, with greater change in core body temperature occurring during the summer (0.92°C, 95% *CI* = 0.87–0.97°C) than in winter (0.58°C, 95% *CI* = 0.53–0.63°C; Fig. 3B; Wald χ^2 = 533.18, *P* < 0.001). Ambient temperature, precipitation, solar radiation, and wind influenced the daily change in core body temperature (Table 1; Supplementary Data SD5), with solar radiation and ambient air temperature accounting for 0.17–0.20°C of the variation in daily change in core body temperature over the range of the environmental variables (Table 2). Time of day for both maximum (Wald χ^2 = 313.98, *P* < 0.001) and minimum (Wald χ^2 = 813.89, *P* < 0.001) core body temperature showed seasonal variation, with maximum and minimum observations occurring later in the day during
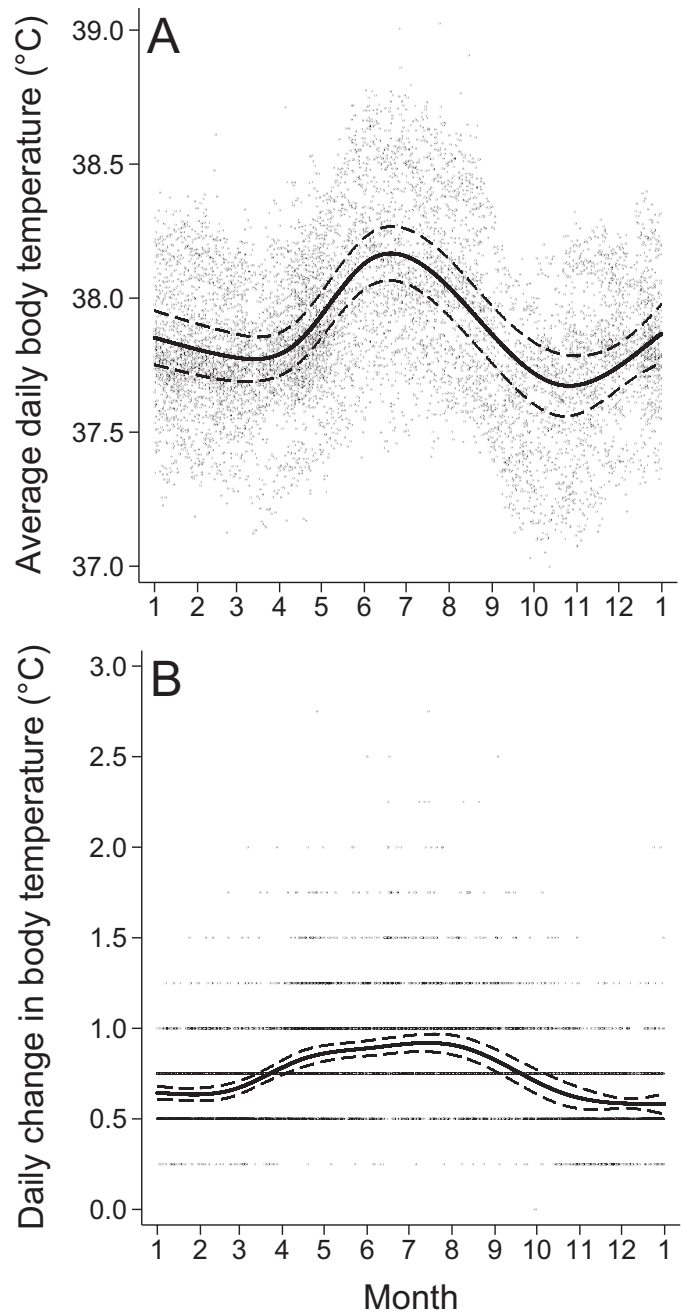

Fig. 3.—Annual variation in core body temperature of female moose (*Alces alces*). Core body temperatures were measured between 16 November 2014 and 5 December 2017 in both free-ranging captive moose (*n* = 11) at the Kenai Moose Research Center and wild moose (*n* = 25) on the Kenai Peninsula, Alaska. A) Observed daily average core body temperature (dots), with values (solid line with dashed lines for 95% confidence intervals) predicted from mixed model regression against time (Julian date). B) Observed daily change in core body temperature (dots), with values (solid line with dashed lines for 95% confidence intervals) predicted from mixed model regression against time (Julian date).

the summer than in winter (Fig. 4). Ambient air temperature influenced the time of day at which maximum and minimum core body temperature occurred (Table 1; Supplementary Data SD6 and SD7). Solar radiation, vapor pressure, and wind speed

Table 2.—Selected models of the relationship between environment and core body temperature recorded in free-ranging captive and wild moose (*Alces alces*) on the Kenai Peninsula, Alaska from November 2014 through December 2017. The effect of each environmental variable on core body temperature is predicted at the observed minimum (MIN) and maximum (MAX) value for the model variable with the absolute range of the response ($\Delta = $ |MAX − MIN|). Models are selected from a suite of multiple linear regression models in Supporting Information SD4–SD7. Δ = daily range; Σ = daily total; $\bar{x}$ = daily mean.

Response variable	Model variable	Observed range of model variable		Predicted effect on response variable		
		MIN	MAX	MIN	MAX	Δ
Residuals – daily average core body temperature (°C)						
	$\bar{x}$ Ambient temperature (°C)	−23.3	19.8	0.03	−0.03	0.06
	Δ Ambient temperature (°C)	1.3	24.3	0.03	−0.05	0.08
	Δ Vapor pressure (hPa)	0.2	9.0	−0.03	0.06	0.09
Residuals – daily change in core body temperature (°C)						
	Δ Ambient temperature (°C)	1.3	24.3	−0.07	0.12	0.19
	Σ Precipitation (mm)	0.0	32.1	0.01	−0.09	0.10
	$\bar{x}$ Solar radiation (W/m^2)	0.0	355.0	−0.05	0.15	0.20
	Δ Solar radiation (W/m^2)	0.0	1,128.0	0.07	−0.10	0.17
	$\bar{x}$ Wind speed (m/s)	0.0	3.8	−0.01	0.06	0.07
Residuals – time of day of maximum core body temperature (h)						
	$\bar{x}$ Ambient temperature (°C)	−23.3	19.8	3.04	−2.23	5.27
	$\bar{x}$ Solar radiation (W/m^2)	0.0	355.0	−0.75	1.63	2.38
	$\bar{x}$ Vapor pressure (hPa)	0.8	15.7	−0.82	1.11	1.93
	$\bar{x}$ Wind speed (m/s)	0.0	3.8	0.17	−1.04	1.21
Residuals – time of day of minimum core body temperature (h)						
	$\bar{x}$ Ambient temperature (°C)	−23.3	19.8	1.13	−0.94	2.07
	Δ Ambient temperature (°C)	1.3	24.3	−0.95	1.16	2.11
	Σ Precipitation (mm)	0.0	32.1	−0.04	−2.09	2.05
	$\bar{x}$ Solar radiation (W/m^2)	0.0	355.0	−0.54	1.08	1.62
	$\bar{x}$ Wind speed (m/s)	0.0	3.8	0.34	−1.56	1.90

also influenced time of day for maximum core body temperature (Table 1; Supplementary Data SD6), while precipitation also influenced time of day for minimum core body temperature (Table 1; Supplementary Data SD7). Mean ambient air temperature accounted for the greatest variation in time of day for maximum core body temperature (5.27 h over the range of mean ambient air temperature; Table 2), while both ambient air temperature and precipitation accounted for the greatest variation in minimum core body temperature (2.05–2.11 h over the range of the environmental variables; Table 2).

Maximum rump fat thickness decreased from early winter (3.6 ± 0.9 cm; mean ± *SD*) to spring (1.2 ± 0.7 cm). Declines in IFBFAT resulted in an increase in daily change in core body temperature (Fig. 5A; $z = −5.73$, $P < 0.001$), a decrease in minimum daily core body temperature (Fig. 5B; $z = 4.61$, $P < 0.001$), and a decrease in average daily core body temperature ($z = 4.01$, $P < 0.001$). However, IFBFAT did not influence daily maximum core body temperature ($z = 0.82$, $P = 0.414$).

DISCUSSION

Daily average core body temperature of adult female moose followed the seasonal patterns described for food intake, activity, and fasting metabolic rate in moose that were highest in summer and lowest in winter (Schwartz et al. 1984; Regelin et al. 1985; Renecker and Hudson 1985, 1986a; Bevins et al. 1990). This seasonal pattern of average daily core body temperature in moose is consistent with the hypothesis for hypothermia-induced heterothermy that minimizes or reduces the cost of thermoregulation in winter when food supplies are

lowest and metabolic rates are suppressed (Hetem et al. 2016). Daily core body temperature of female moose followed an annual pattern similar to other ungulates (Fig. 3A; Fuller et al. 2005; Hetem et al. 2010; Signer et al. 2011; Turbill et al. 2011; Arnold et al. 2018). In small mammals, daily activity patterns are similar to daily body temperature patterns (Goh et al. 2019), but this inherent similarity many not indicate that body temperature is a response to activity (Refinetti 2010). Further research relating activity and core body temperature in moose is warranted. The frequency distribution of core body temperature is narrow for moose (Fig. 2), similar to that measured for pronghorn in a temperate climate (Lust et al. 2007; Hébert et al. 2008), and for blesbok (*Damaliscus phillipsi*) in Africa (Hetem et al. 2016). The frequency distribution of core body temperature in moose was narrower than that of Arabian oryx (*Oryx leucoryx*), which employs hyperthermia-induced heterothermy in response to high ambient temperatures, resulting in a large range of core body temperature (Hetem et al. 2010, 2016).

Contrary to the hypothermia-induced heterothermy hypothesis, daily change in core body temperature of moose was greater during the summer than the winter (Fig. 3B). Daily change in rumen temperature in alpine ibex also showed a seasonal shift; however, a greater daily change in rumen temperature was observed in winter (Signer et al. 2011). The lower daily change in core body temperature in winter for moose could be a result of their low surface area to volume ratio and high insulation properties of their winter coat (Scholander et al. 1950), which would minimize loss of heat from the body to the environment. High daily change in core body temperature observed in moose during the summer may be associated with
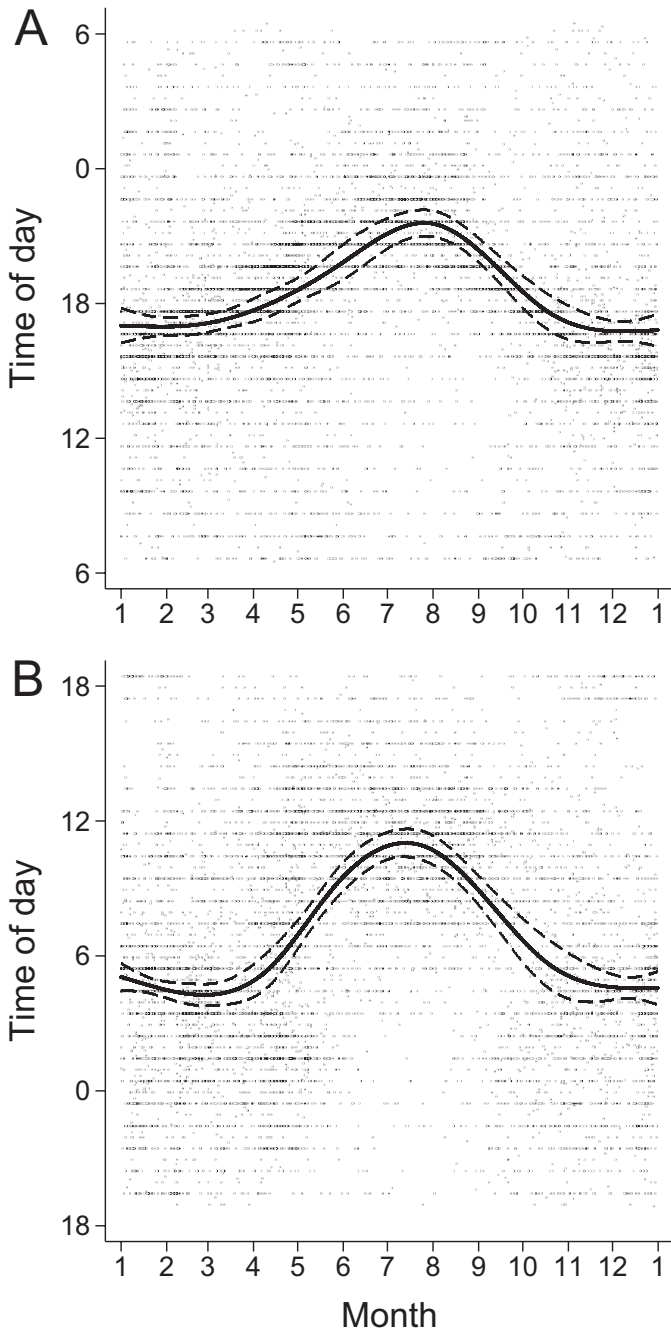
Fig. 4.—Annual variation in the diurnal pattern of body temperature in female moose (*Alces alces*). Maximum and minimum core body temperatures were measured in free-ranging captive (*n* = 11) and wild (*n* = 25), adult female moose between 16 November 2014 and 5 December 2017 on the Kenai Peninsula, Alaska. A) Observed time of day for maximum core body temperature (dots), with values (solid line with dashed lines for 95% confidence intervals) predicted from mixed model regression against time (Julian date) centered on the daily circular mean time of day for maximum core body temperature (18:50). B) Observed time of day for minimum core body temperature (dots), with values (solid line with dashed lines for 95% confidence intervals) predicted from mixed model regression against time (Julian date) centered on the daily circular mean time of day for minimum core body temperature (07:01).
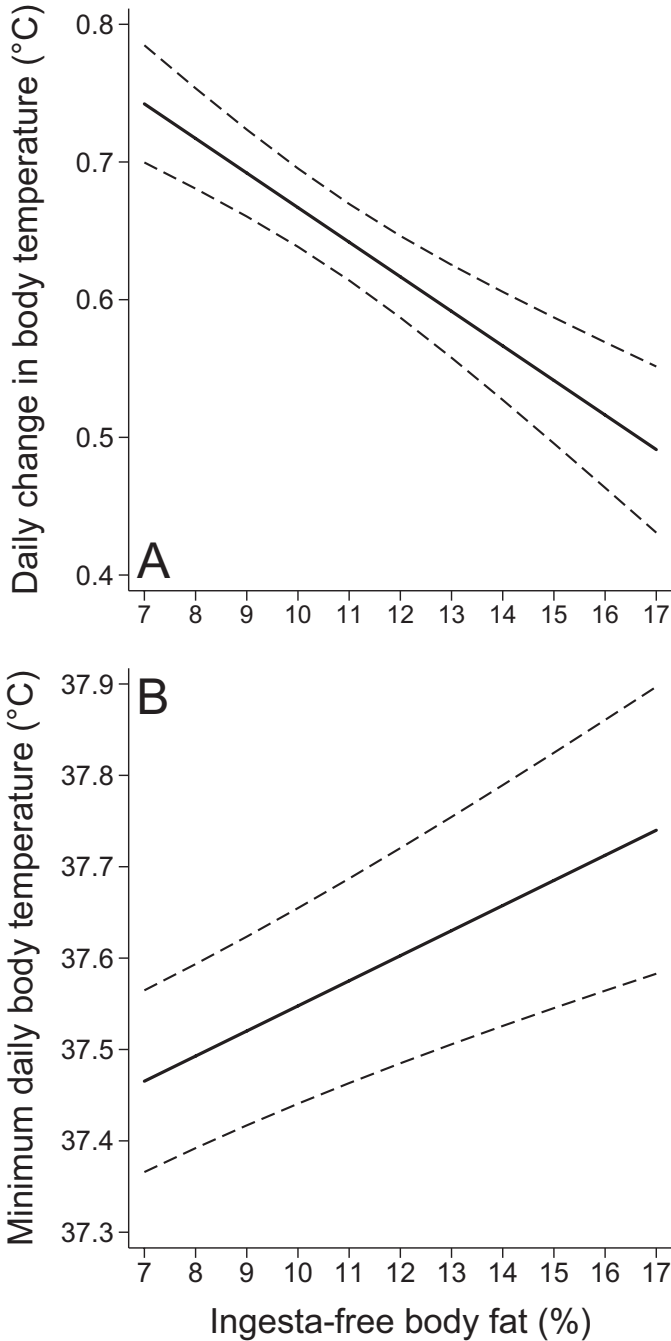
Fig. 5.—Linear effects (solid lines with dashed lines for 95% confidence intervals) of body condition (% ingesta-free body fat) on core body temperature of both free-ranging captive moose (*Alces alces*; *n* = 5) at the Kenai Moose Research Center and wild moose (*n* = 11) on the Kenai Peninsula, Alaska from 1 December 2014 to 1 March 2015. A) Daily change in core body temperature, and B) minimum daily core body temperature.

high rates of forage intake during the growing season for plants (Renecker and Hudson 1986b). The heat increment of feeding (Secor 2009) rises with forage intake to produce metabolic heat that could increase both daily mean and change in core body temperature. Moose must be able to dissipate this endogenous

heat load quickly by ingesting water or selecting microclimates to increase heat loss to the environment (Olson et al. 2014; Street et al. 2015; McCann et al. 2016; Herberg et al. 2018). We did record a maximum daily change in core body temperature for moose of 3.5°C; however, the mean daily change in core body temperature of moose during summer was considerably lower than the large daily changes in core body temperature seen in Arabian antelope, which rely on hyperthermia-induced heterothermy to conserve body water (Hetem et al. 2010, 2012). Because moose live in areas that typically are not limited by water, hyperthermia-induced heterothermy would risk the negative effects of hyperthermia without significantly improving fitness by conserving body water.

Moose exhibited a daily rhythm in core body temperature similar to other ungulates (Figs. 3B and 4; Fuller et al. 2005; Lust et al. 2007; Hetem et al. 2010; Signer et al. 2011; Shrestha et al. 2012); daily maximum body temperature was attained in the late afternoon and evening, whereas daily minimum body temperature was achieved before noon. We also documented a seasonal shift in the time of day that minimum and maximum core body temperature occurred, which has also been documented in alpine ibex and Arabian sand gazelles (*Gazella subgutturosa marica*— Ostrowski and Williams 2006; Signer et al. 2011). During the summer, our data for the time of day that minimum core body temperature occurred corresponded to the same time of day (mid-morning) when moose in Finland select the densest cover (Melin et al. 2014), which would imply that moose may be selecting thermal refuges that enable their body temperature to continue to decline to the daily nadir even though ambient air temperature is increasing. Furthermore, our data for the time of day when maximum core body temperature occurred in the summer indicates that moose reached daily maximum core body temperature later in the day (~21:00 h), which would indicate moose are accumulating a heat load into the evening during the warmest part of the year (Fig. 1A). Moose may dissipate this heat load through nighttime cooling to reduce core body temperature as documented in cattle (Mader and Davis 2004; Scharf et al. 2011).

Pregnant moose had a lower daily change in core body temperature than non-pregnant moose (Supplementary Data SD2 and SD3); however, the difference between pregnant and non-pregnant animals was < 0.2°C, which was within the accuracy of the temperature logger. Increased metabolism during gestation has been observed in other cold-adapted ungulates (Pekins et al. 1998) and our data suggest that is also evident in moose (Supplementary Data SD2 and SD3). In domestic cattle, brown bears (*Ursus arctos*), and African lions (*Panthera leo*), pregnant animals had a lower daily change in core body temperature than non-pregnant animals (Kendall and Webster 2009; Friebe et al. 2014; Trethowan et al. 2016). Small variations in daily change in core body temperature between pregnant and non-pregnant moose may be difficult to discern in randomly caught wild moose as high pregnancy rates would skew sample sizes towards pregnant animals (Testa and Adams 1998; Keech et al. 2000; Milner et al. 2012; Murray et al. 2012). Additionally, female moose that have high body reserves (e.g., ingesta-free body fat) have high pregnancy rates (Testa and Adams 1998; Keech et al. 2000), while female moose with low body reserves may not become pregnant, and any differences in daily change in core body temperature between pregnant and non-pregnant female moose may be a function of body reserves rather than specific physiological responses to pregnancy.

As suggested by the hypothermia-induced heterothermy hypothesis, the ability for moose to maintain core body temperature during winter was influenced by body reserves. Our assumption of a linear decline between two estimates of ingesta-free body fat probably underestimated the rate at which energy is used to maintain average daily core body temperature during cold days because the daily rate of fat loss in winter is probably not constant; however, immobilizing wild moose to collect more than two measures of body fat from the same animal during one season was not feasible. Although the predicted responses of daily change in core body temperature and the minimum daily core body temperature with body fat were small (Fig. 5), the slope of the statistical relationship was consistent with a negative relationship between body reserves and energy expenditure for thermoregulation. Our estimates of 23–74 kg of ingesta-free body fat (Stephenson et al. 1998) would be equivalent to 903–2,908 MJ of body reserves at 39.3 kJ/g of lipid (Barboza et al. 2009). Moose with low body reserves may be diverting energy away from thermoregulation during winter but may be able to compensate by endogenous or exogenous factors to conserve energy. State-dependent foraging has been documented in moose in the southern portion of their range, that is, moose with lower body reserves also had higher indices of energy intake in winter than those with high body reserves (Jesmer et al. 2017). High energy intake could enhance metabolic heat produced from feeding in moose (144–216 kJ kg^{-75} day^{-1}; Renecker and Hudson 1986a) to rewarm core body temperature and decrease thermoregulatory costs (Jensen et al. 1999; Lawler and White 2003; Crater and Barboza 2007). Moose with lower body reserves also may select habitat that allows for solar radiation to rewarm the body from the nightly low (Signer et al. 2011) or select habitats that provide thermal cover to decrease heat loss (Long et al. 2014).

Each environmental variable accounted for small but significant amounts of variation in metrics of core body temperature of moose (Table 2); however, the effects of each environmental parameter may be additive or subtractive when combined with the other parameters. Days with high vapor pressure may decrease the efficiency of evaporative heat loss through the respiratory tract in moose, resulting in an increase in core body temperature (Gates 1980; Silanikove 2000). High winds can disrupt the thermal pocket of air trapped within the hair coat that provides insulation, which would increase convective heat loss and could lower core body temperature (Gates 1980; Silanikove 2000). The dark pelage of moose may absorb solar radiation and thus increase daily change in core body temperature (Cain et al. 2006), particularly during the summer when moose hair is short and solar radiation is at its peak. Furthermore, considering that moose do not actively sweat, any precipitation

that would dampen the skin surface could increase evaporative heat loss, influencing daily change in core body temperature. In domestic livestock, core body temperature was lowered by high levels of precipitation in sheep (*Ovis aries*) or by using sprinklers in dairy cattle (Lowe et al. 2001; Kendall et al. 2007). Additionally, changes in ambient temperature can shift the time of day that maximum core body temperature occurs in domestic sheep (Piccione et al. 2013), similar to the variation we observed in time of day for maximum body temperature in moose.

Implications of hypothermia-induced heterothermy in a large-bodied endotherm.—Our understanding of variation in body temperature in moose is essential for managing populations where exposure to warm seasonal temperatures is increasing and is a topic of heightened concern for moose (Murray et al. 2006; Monteith et al. 2015). Our study demonstrates that adult female moose exhibit some traits of hypothermia-induced heterothermy based on seasonal variation in core body temperature and body reserves. Given the daily and seasonal variations in core body temperature that we documented, core body temperature of moose still fluctuates within a narrow range (Fig. 2). When studying the influence of environmental stressors on northern cervids, researchers should consider the daily rhythm in core body temperature because physiological and behavioral responses may be different in the morning at the daily nadir of core body temperature compared with responses in the evening at the daily peak of core body temperature. Endogenous variation in core body temperature provides a context for assessing heat stress in moose because deviations from homeothermy are often misidentified as indicators of heat stress (Levesque et al. 2016). Examining core body temperature, in concert with the daily amplitudes in core body temperature, could be used to determine when moose are responding to warm environmental temperatures (Levesque et al. 2016; Mitchell et al. 2018). By improving our understanding of how moose respond to warm temperatures, we can move away from analyzing moose habitat and movements using upper critical temperature thresholds (Renecker and Hudson 1986a; McCann et al. 2013) that can "overestimate massively the risk of thermal peril under climate change" (Mitchell et al. 2018: 965). Improved criteria for determining heat stress can be used to resolve behavioral indices of heat stress and identify environmental patterns that increase the risk to female moose from heat stress, increasing the vulnerability of their population to warming.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Ranking of mixed model regressions using Akaike's information criterion (AICc; corrected for small sample size) for average daily core body temperature recorded in free-ranging captive ($n = 11$) and wild ($n = 25$) adult female moose (*Alces alces*) on the Kenai Peninsula, Alaska from November 2014 through December 2017.

Supplementary Data SD2.—Selected model for daily average core body temperature recorded in free-ranging captive ($n = 11$) and wild ($n = 25$) adult female moose (*Alces alces*) on the Kenai Peninsula, Alaska from November 2014 through December 2017.

Supplementary Data SD3.—Annual variation in average daily core body temperature of female moose (*Alces alces*). Core body temperatures were measured between 16 November 2014 and 5 December 2017 in both free-ranging captive moose ($n = 11$) at the Kenai Moose Research Center and wild moose ($n = 25$) on the Kenai Peninsula, Alaska.

Supplementary Data SD4.—Ranking of regression models using Akaike's information criterion (AICc; corrected for small sample size) for residuals of average daily core body temperature (Fig. 3A) recorded in free-ranging captive ($n = 11$) and wild ($n = 25$) adult female moose (*Alces alces*) on the Kenai Peninsula, Alaska from November 2014 through December 2017.

Supplementary Data SD5.—Ranking of regression models using Akaike's information criterion (AICc; corrected for small sample size) for residuals of daily change in core body temperature (Fig. 3B) recorded in free-ranging captive ($n = 11$) and wild ($n = 25$) adult female moose (*Alces alces*) on the Kenai Peninsula, Alaska from November 2014 through December 2017.

Supplementary Data SD6.—Ranking of regression models using Akaike's information criterion (AICc; corrected for small sample size) for residuals of time of day when maximum core body temperature occurred (Fig. 4A) in free-ranging captive ($n = 11$) and wild ($n = 25$) adult female moose (*Alces alces*) on the Kenai Peninsula, Alaska from November 2014 through December 2017.

Supplementary Data SD7.—Ranking of regression models using Akaike's information criterion (AICc; corrected for small sample size) for residuals of time of day when minimum core body temperature occurred (Fig. 4B) in free-ranging captive ($n = 11$) and wild ($n = 25$) adult female moose (*Alces alces*) on the Kenai Peninsula, Alaska from November 2014 through December 2017.

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