Behaviour influences thermoregulation of boreal moose during the warm season

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Management of large herbivores depends on providing habitats for forage supply and refuge from risks of temperature, predation and disease. Moose (Alces alces) accumulate body energy and nutrient stores during summer, while reducing the impact of warm temperatures through physiological and behavioural thermoregulation. Building on the animal indicator concept, we used rumen temperature sensors and GPS collars on captive moose (n = 6) kept in large natural enclosures to evaluate how behaviour and habitat selection influence the rate of change in rumen temperature during the growing season on the Kenai Peninsula, Alaska, USA. We compared movement and habitat selection of individual females during tolerance days (daily amplitude in rumen temperature was ≥1.2°C in 24 h) with those of control days (daily amplitude in rumen temperature was < 1.2°C) before and after the tolerance day. Moose moved more during tolerance days (172 m • h−1; 95% confidence intervals (CI) = 149–191 m • h−1) than on control days (151 m • h−1; 95% CI = 128–173 m • h−1). The rate of change in rumen temperature (°C • h−1) declined with low to moderate movement rates that were probably associated with foraging in all habitats. Movement only increased the rate of change in rumen temperature at high activity (~ > 500 m • h−1). Additionally, the relationship between rate of change in rumen temperature and movement rate was different during tolerance and control days in open meadow and wetland habitats. In all habitats except wetlands, the rate of change in rumen temperature increased while resting, which probably is a result of diet-induced thermogenesis. Our study demonstrates that the behavioural choices of moose on the landscape are associated with the rate of change in rumen temperature and their ability to thermoregulate. Wildlife managers must consider high-value habitats where wildlife can employ both behavioural and physiological mechanisms to tolerate warm ambient conditions in a landscape of forage, predators and pests.

Key words: Activity, Alaska, Alces alces, behaviour, moose, rumen temperature, thermoregulation

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Introduction

The ability for wildlife to obtain, utilize and conserve energy and protein for maintenance, growth and reproduction varies based on the species and the landscape they inhabit (Barboza et al., 2009). The value of the landscape for an animal depends on trade-offs between food supplies, environmental demands and risks of injury or death (e.g. movement, food quality and quantity, environmental conditions and predation risk; Laundré et al., 2001; Wilson et al., 2012; Long et al., 2016; Gallagher et al., 2017). Fluctuations in environmental temperatures can influence an animal’s movement and food intake (McFarland et al., 2014; Camp et al., 2018; Haase et al., 2019) and activate physiological, behavioural and endocrine responses for thermoregulation (Silanikove, 2000; Cain III et al., 2006; Terrien et al., 2011). Animals may alter their behaviour to reduce their exposure to unfavourable environmental conditions (e.g. burrowing; Fick et al., 2009) or to alleviate a current thermoregulatory demand (e.g. drinking; Brain and Mitchell, 1999). Behavioural responses to warm environmental temperatures in ungulates include solar orientation of the body (Maloney et al., 2010), decreasing or shifting activity patterns (Maloney et al., 2005a; Shrestha et al., 2014; Boyers et al., 2019) and selecting habitats on the landscape that provide access to shade, water or wind (Valeix et al., 2008; Hetem et al., 2012; Wiemers et al., 2014; McCann et al., 2016). The actual thermoregulatory benefit to the animal from these behavioural responses can only be assessed without simultaneously monitoring the subsequent effect on body temperature.

Continuous body temperature measurements have been collected in wild ungulates through biologging technology (Fuller et al., 2005; Signer et al., 2010; Rey et al., 2016; Thompson et al., 2018). Following the animal indicator concept (Franzmann, 1983), continuous body temperature measurements could be used as a physiological indicator for an animal’s relationship with their environment (Thompson et al., 2020). Prior studies have documented core body temperature in conjunction with activity levels in ungulates (Turbill et al., 2011; Rick et al., 2017; Arnold et al., 2018; Boyers et al., 2019) but did not evaluate how activity or behaviour is associated with body temperature. Burrow use of Arctic ground squirrels (Spermophilus parryii) influenced core body temperature (Long et al., 2005), while core body temperature was influenced by swimming, drinking and sand bathing in African primates (Brain and Mitchell, 1999; McFarland et al., 2019). The effects of a warming climate on behaviour have been documented in northern ungulates (Long et al., 2014; Brivio et al., 2019; Jennewein et al., 2020); however, the behavioural implications of these choices for maintaining body temperature have not been tested. We studied how behaviour is associated with body temperature in moose (Alces alces), a cold-adapted ungulate, to understand the effects of thermal trade-offs for a large animal in a warming climate.

Moose are generally solitary animals that rely on high forage intakes during the short, warm season to accumulate body energy and protein reserves (Schwartz et al., 1984; Shively et al., 2019), with ~75% of activity associated with foraging during this time frame (Bullenbergh and Miquelle, 1990; Herberg, 2017). As environmental temperatures increase, activity levels of moose decrease and may shift to a nocturnal activity pattern (Demarchi and Bunnell, 1995; Dussault et al., 2004; Street et al., 2015; Montgomery et al., 2019; Jennewein et al., 2020). Additionally, moose respond to warm ambient temperatures at both the landscape level by selecting forested habitat types for thermal cover and wetland areas (Renecker and Hudson, 1990; Dussault et al., 2004; Broders et al., 2012; van Beest et al., 2012; Street et al., 2015; Wattles et al., 2018; Alston et al., 2020; Jennewein et al., 2020) and at a microhabitat level by selecting resting sites that increase heat loss (McCann et al., 2016; Olson et al., 2016). We recently validated devices to continually log core temperature in moose (Herberg et al., 2018; Thompson et al., 2018) and subsequently established daily and seasonal core body temperature patterns for moose (Thompson et al., 2019). Combining continuous body temperature measurements of moose, with movement and habitat selection may allow us to evaluate the relationship between the individual animal and their daily trade-offs on the landscape.

Following the animal indicator concept, we used internal body temperature sensors and GPS collars on captive moose to evaluate if behavioural choices are associated with the rate of change in rumen temperature during the growing season on the Kenai Peninsula, Alaska. Here, we expand on our prior research in which we use the individual daily amplitude in core body temperature to determine when moose tolerate fluctuations in daily core body temperature above established seasonal values (Thompson et al., 2020). We identify individual ‘tolerance’ days as a day in which an individual moose rumen temperature had a daily amplitude ≥1.2°C (tolerance day = heat response day in Thompson et al., 2020). Therefore, we consider a control day as the day prior and day after a ‘tolerance’ day in which that individual moose’s rumen temperature had a daily amplitude <1.2°C. We hypothesize that (i) the daily patterns in hourly rate of change in rumen temperature, movement rates and drinking for moose would differ between a tolerance day and a control day. During a tolerance day, we predict moose would exhibit an increased rate of change in rumen temperature compared to a control day. Additionally, on tolerance days, we predict moose would reduce movement rates and increase drinking events in the late afternoon and early evening as body temperature, ambient air temperature and vapour pressure typically rise (Thompson et al., 2020). Furthermore, we hypothesize that (ii) the rate of change in moose rumen temperature is dependent on movement rates and habitat selection and would differ between tolerance and control days. We predict that moose will decrease movement rates and select habitats (e.g. wetlands) that would decrease the rate of change rumen temperature.
temperature on tolerance days. We also evaluated habitat selection by moose to determine if activity within habitats and resting site selection varied between tolerance and control days. We hypothesize that (iii) moose activity status (resting and active) would change within habitats during tolerance and control days. We predict that the time of day in which moose would select typically cool habitats (e.g. wetlands) would change during a tolerance day, with a higher probability of selection during resting bouts. Finally, we hypothesize that (iv) moose would select resting sites based on microhabitat attributes, which would aid in thermoregulation. We predict moose would select resting sites during tolerance days that contained microhabitats, which would be elevated (i.e. access to wind) and have higher canopy cover than the immediate surrounding habitat.

Materials and methods

Study site

We studied free-ranging (i.e. kept in a natural conditions) captive moose on the Kenai Peninsula, Alaska, USA. Moose were held in two 2.6 km² outdoor enclosures at the Kenai Moose Research Center, operated by the Alaska Department of Fish and Game on the Kenai National Wildlife Refuge. We used an orthorectified aerial photo (Nikon D800; resolution, 7360 × 4912; focal length, 24 mm; pixel size, 4.88 × 4.88 μm; flight, 24 April 2015; elevation, 629 m; U.S. Fish and Wildlife Service, Kenai National Wildlife Refuge) to manually digitize vegetation polygons within each enclosure (ArcGIS 10.6; ESRI, Redland, CA, USA). We classified vegetation polygons as early-seral boreal forest (2–5 years post-disturbance, open canopy), mid-seral boreal forest (25 years post-disturbance), old growth boreal forest (65+ years post-disturbance), black spruce forest, wetland (kettle ponds and/or sphagnum peat bogs with areas of standing water) and open meadow. One enclosure also contained a 0.16 km² lake. Vegetation classifications were sampled for tree density and to identify understory species (Supplementary Data S1).

Environmental conditions

Ambient air temperature (°C), precipitation (mm), wind speed (m • s⁻¹), solar radiation (W • m⁻²) and relative humidity were recorded every 5 min at a National Oceanic and Atmospheric Administration (NOAA) US Climate Reference Network weather station located at the Kenai Moose Research Center (Diamond et al., 2013). Relative humidity and ambient air temperature were used to calculate dew point temperature (°C) and vapour pressure (hPa; Alduchov and Eskridge, 1996). We recorded ambient air temperature every 5 min in the six habitat types with Thermochron iButtons (accuracy, 0.5°C; Model DS1922L#F50; Maxim Integrated, San Jose, CA, USA) placed in yellow iButton key ring mounts (Model DS9093AY; Maxim Integrated). We suspended iButtons (n = 30; five in each habitat) from an i-bolt 120 cm off the ground and 10 cm from the north side of trees in forested habitats or from a steel T-post in open habitats. iButtons were strategically placed within each habitat type to collect representative data and to cover the study area. Additionally, we suspended five iButtons on the NOAA weather station to validate the iButtons. We used new iButtons at the start of the study that were calibrated by the manufacturer.

Animal handling

We chemically immobilized adult, non-reproductive female moose (≥ 2 years old; n = 6) in December 2014 using procedures detailed in Herberg et al. (2018). While moose were immobilized, we fitted an Iridium global positioning system (GPS) collar (0.5 h fix rate; GPS Plus-7; Vectronic Aerospace GmbH; Berlin, Germany) and deployed a mortality implant transmitter as a rumen bolus (accuracy, 0.1°C; Vectronic Aerospace GmbH, Berlin, Germany; Minicucci et al., 2018). Mortality implant transmitters recorded reticulorumen (hereafter rumen) temperature approximately every 5 min that we previously validated with these same moose (Herberg et al., 2018). Rumen temperature was transmitted and stored on the GPS collar. All procedures for animal care, handling and experimentation were approved by the Animal Care and Use Committee, Alaska Department of Fish and Game, Division of Wildlife Conservation (protocol no. 09-29 and protocol no. 2014-17) and Texas A&M AgriLife Research Agricultural Animal Care and Use Committee (AUP# 2016-008A).

Data analysis

We evaluated data collected during the warm season from 1 May 2015 to 31 August 2015. Rumen temperature was recorded approximately every 5 min but did not always correspond to the 5 min demarcations for all other measurements; therefore, we linearly interpolated rumen temperature to align with the rest of the dataset (Herberg et al., 2018). Additionally, we linearly interpolated rumen temperature for any missing values (<2% of rumen temperature records). We identified drinking events (n = 794) as dips in rumen temperature below 37.5°C and the subsequent 40 min as rumen temperature returned to within one standard deviation of the initial rumen temperature (Herberg et al., 2018). Additionally, we flagged any drop in rumen temperature > 0.2°C within 5 min as a drinking event (Arnold et al., 2018). We created a binary variable with 0 as no drinking event and 1 as a drinking event to censor the temperature record. To establish directional changes in body temperature, we linearly interpolated the rumen temperature for data that was flagged as a drinking event. We determined the rate of change in rumen temperature (°C • h⁻¹) by subtracting the rumen temperature 0.5 h prior from the current rumen temperature. We identified tolerance days for individual moose as days in which their rumen temperature, after removing drinking events, had a daily amplitude ≥ 1.2°C (Thompson et al., 2020). For statistical comparison, we created a categorical variable for daily thermoregulatory response with two levels: tolerance day and control day based on individual daily amplitude in rumen temperature.
We removed moose locations if the GPS horizontal dilution of precision was ≥10 m (0.4% of GPS points) and replaced those locations by linear interpolation of the coordinates from acceptable locations before and after. We calculated movement rate (m $\cdot$ h$^{-1}$) for each successive 0.5 h location. We transformed the continuous variable of movement rate with a natural log and then used a spline fit (seven-knot spline based on percentiles for large sample sizes; Harrell, 2001) for the model assessing if movement rate is associated with the rate of change in rumen temperature. To delineate potential resting sites for moose, we flagged all GPS locations with a movement rate ≤15 m $\cdot$ 0.5 h$^{-1}$ based on the estimated GPS error from other studies (Lowe, 2009; McCann et al., 2016). For habitat analyses, we created the categorical variable activity status with two categories: resting (movement rate <15 m $\cdot$ 0.5 h$^{-1}$) and active (movement rate ≥15 m $\cdot$ 0.5 h$^{-1}$). We spatially joined moose locations from the GPS collars with vegetation polygons (ArcGIS Pro 2.4.2; ESRI, Redland, CA, USA). We reclassified any moose GPS location in the lake to wetland. Additionally, any GPS location that fell outside of an enclosure was reclassified as the habitat closest to it within the enclosure (e.g. a moose was next to the enclosure fence and the GPS location was outside of the enclosure). We created binary variables for each habitat type to analyse probability of use.

We used light detection and ranging data (LIDAR; 1.2 m resolution; 2008; Kenai Peninsula Borough, Geographic Information Systems) to assess microhabitats associated with topography (digital elevation model) and canopy cover (digital surface model) around each moose GPS location. Using the package exactextractr (Baston, 2019) in R (R Core Team, 2018), we determined the mean value and raster pixel count in a 5 m and 25 m radius around each GPS location for both the digital elevation model and the digital surface model. We spatially joined the elevation value from the digital elevation model with each moose GPS location. To determine if the GPS location was above or below the surrounding area, we standardized the metric by subtracting the value for the mean elevation of the 5 m radius around the elevation of the GPS location. We used the digital surface model to estimate canopy cover surrounding each location in the forested habitats. We limited digital surface model data to values ≥1.5 m (i.e. above the height of a bedded moose) and assigned a value of 0.0 m to all early-seral vegetation polygons that were early-seral boreal forest as a result of habitat improvements after the LIDAR data were collected. We determined percent canopy cover for each GPS location by dividing the area within either the 5 m or 25 m radius that had a digital surface model value greater than 1.5 m, by the total area of the 5 m or 25 m radius from the digital elevation model, respectively.

We analysed data using programs in STATA version 15.0 (StataCorp LP, College Station, Texas, USA). We used simple linear regression to establish a relationship between ambient air temperature recorded with iButtons located at the weather station and iButtons located at the weather station. To evaluate the dependent variable of ambient temperature recorded with iButtons within each habitat, we used mixed model regression with the independent categorical variables of habitat type (six categories), time of day (0.5 h time periods starting at 0:00) and the interaction of habitat type and time of day. Using mixed model regression, we evaluated if the dependent variables (rate of change in rumen temperature; movement rate) were associated with the independent categorical variables of daily thermoregulatory response (control day vs. tolerance day), time of day and the interaction between daily thermoregulatory response and time of day. Similarly, we used mixed-effects logistic regression to determine if the probability of a drinking event was associated with the independent categorical variables of daily thermoregulatory response, time of day and their interaction. To evaluate if the dependent variable rate of change in rumen temperature was affected by movement rate and habitat selection, we used mixed model regression with the independent categorical variables for habitat type and daily thermoregulatory response, the two-way interaction of the categorical variables and the continuous variable for movement rate. Based on the results of this analysis, we further evaluated if movement rate and daily thermoregulatory response was associated with the change in rumen temperature in each specific habitat with mixed model regression. To determine the probability of moose selecting each habitat, we used mixed-effect logistic regression with the independent categorical variables daily thermoregulatory response, activity status (active and resting), time of day and all two- and three-way interactions of the independent variables. For microhabitat selection, we used mixed model regression for the three dependent variables (elevation of resting site; percent canopy cover of 5 m and 25 m radius) to determine if they were associated with the independent categorical variables daily thermoregulatory response, habitat type and the interaction of the independent variables. All mixed model regressions and mixed-effect logistic regressions included individual as a random effect. We reduced the effects of heteroscedacity and non-normal distributions with a robust sandwich estimator (Rabe-Hesketh and Skrondal, 2010). We examined linear fixed effects with a Wald test, and model explanatory variables were compared with zero using a z-test at $P < 0.05$. We then estimated marginal means (mean ± 95% confidence interval) to determine significant differences in the levels for each categorical variable. We performed model selection on all mixed and logistic regression models for physiological and behavioural responses in moose using Akaike’s information criterion, adjusted for small sample sizes (AICc). We selected the simplest model with the lowest AICc within two AICc units of the top model (Burnham and Anderson, 2002).

**Results**

**Environmental conditions**

Early summer was cool and dry with daily low values of ambient air temperature (lowest daily minimum, −3.8°C;
Ambient air temperature recorded with iButtons suspended on the weather station was similar to ambient air temperature recorded by the NOAA weather station sensor ($y = 1.15x - 0.93; F_{1,164,395} = 999999.0; P < 0.001; r^2 = 0.96$). Daily ambient air temperature patterns differed by habitats ($Wald \chi^2 = 48991.7, P < 0.001$); daily variation in open meadow and wetlands were greater than those of mid- and late-seral boreal forest (Fig. 1).

**Rumen temperature and behaviour**

We flagged 139 individual tolerance days (19% of all individual moose days) when the daily amplitude in moose rumen temperature was $\geq 1.2{^\circ}{\text{C}}$. Tolerance days occurred throughout the summer (67 out of 123 days; Supplementary Data S2). When considering time of day and the daily thermoregulatory response, the top model for the rate of change in rumen temperature ($n = 15216$) only included the variable time of day ($Wald \chi^2 = 66.1, P < 0.001$; Supplementary Data S3) with a decreasing rate of change in rumen temperature in the early morning (maximum rate of decrease at 03:30 h; $-0.10{^\circ}{\text{C}} \cdot h^{-1}$; 95% CI = $-0.08$–$-0.14{^\circ}{\text{C}} \cdot h^{-1}$) and increasing rate of change in the evening (maximum rate of increase at 18:30 h; 0.10${^\circ}{\text{C}} \cdot h^{-1}$; 95% CI = 0.06–0.12${^\circ}{\text{C}} \cdot h^{-1}$). Similarly, movement rates ($n = 15216; Wald \chi^2 = 456.2, P < 0.001$; Supplementary Data S3) were highest during the morning (Fig. 2B) and greater on tolerance days (172 m $\cdot$ h$^{-1}$; 95% CI = 149–191 m $\cdot$ h$^{-1}$) than on control days (151 m $\cdot$ h$^{-1}$; 95% CI = 128–173 m $\cdot$ h$^{-1}$). Time of day was the only variable in the top model for the probability of drinking ($Wald \chi^2 = 222.5, P < 0.001$; Supplementary Data S3), which indicated the greatest probability of drinking in the evening (highest probability of drinking at 22:30 h; 0.14; 95% CI = 0.10–0.18; Fig. 2C).

For the model that assessed if habitat selection and movement is associated with the rate of change in rumen temperature, the top model that best described the rate of change in rumen temperature included the categorical variables for habitat type, daily thermoregulatory response, the interaction between habitat type and daily...
Figure 2: Daily patterns of (A) rate of change in rumen temperature (°C • h⁻¹), (B) movement rate (m • h⁻¹) and (C) probability of drinking for captive adult female moose (n = 6) at the Kenai Moose Research Center, Kenai Peninsula, Alaska, USA from May through August 2015. Predicted values with 95% confidence intervals from (A, B) mixed-effect regression and (C) mixed-effect logistic model regression against time of day (0.5 h time periods starting at 0:00). Daily sunrise (04:34–06:56) and sunset (21:13–23:39) varied over the summer. The probability of moose selecting open meadow (Wald \( \chi^2 = 727.3, P < 0.001; \text{Supplementary Data S6} \)) included variables for activity status and time of day. Moose selected open meadow habitat more during the morning and less during mid-day (Fig. 4A), while the probability for selecting open meadow habitat was almost twice as high for resting (0.16, 95% CI = 0.14–0.19) than when active (0.09; 95% CI = 0.07–0.10). The probability of moose selecting black spruce forest (Wald \( \chi^2 = 514.1, P < 0.001; \text{Supplementary Data S6} \)) included the variables for activity status, daily thermoregulatory response and time of day. Moose selected black spruce forest in late morning but had very little use during the night (Fig. 4B). Additionally, the probability of moose selecting black spruce forest was higher when active (0.08, 95% CI = 0.04–0.12) than at rest (0.04; 95% CI = 0.02–0.06), while the probability of moose selecting black spruce forest was marginally higher during tolerance days (0.06, 95% CI = 0.03–0.09) compared to control days (0.05, 95% CI = 0.02–0.07). The probability of moose selecting early-seral boreal forest included the variables for daily thermoregulatory response and the interaction between activity status and time of day (Wald \( \chi^2 = 2671.0, P < 0.001; \text{Supplementary Data S6} \)). The probability of moose selecting early-seral boreal forest was lower on tolerance days (0.35, 95% CI = 0.33–0.37) than on control days (0.39, 95% CI = 0.37–0.41). Furthermore, the probability of moose selecting early-seral boreal forest was greater during early morning than during mid-day, with higher use while active during mid-day compared to resting (Fig. 4C). The probability of moose selecting mid-seral boreal forest (Wald \( \chi^2 = 878.9, P < 0.001; \text{Supplementary Data S6} \)) and late-seral boreal forest (Wald \( \chi^2 = 1286.5, P < 0.001; \text{Supplementary Data S6} \)) included the variables for activity status, daily thermoregulatory response and the continuous variable movement rate (Wald \( \chi^2 = 9800000.0, P < 0.001; \text{Supplementary Data S4} \)). The rate of change in rumen temperature was different for tolerance and control days only in open meadow and wetland habitat types (Supplementary Data S5); however, although statistically significant, these small differences are less than the accuracy of the MIT rumen sensor. Evaluating the relationship between movement rate and rate of change in rumen temperature by each specific habitat, a different response curve between tolerance and control days was only observed in open meadow and wetland habitats (Fig. 3; \( z < 2.49, P < 0.013 \)) compared to the forested habitats. Additionally, the rate of change in rumen temperature varied by movement rate; the rate of change in rumen temperature increased when movement rate was low (e.g. resting) in all habitats except on tolerance days in wetlands (Fig. 3E), while the rate of change in rumen temperature increased in all habitats when movement rate rose above \( \sim > 500 \text{ m} • \text{h}^{-1} \) (Fig. 4).
status and time of day. Moose selected mid- and late-seral boreal forest during mid-day, with lower selection in early morning (Fig. 4D and E). Similarly, the probability of moose selecting both mid- and late-seral boreal forest was higher when active (mid-seral forest = 0.19, 95% CI = 0.16–0.22; late-seral forest = 0.23, 95% CI = 0.20–0.27) than when at rest (mid-seral forest = 0.14, 95% CI = 0.12–0.17; late-seral forest = 0.18, 95% CI = 0.15–0.21). The probability of moose selecting wetlands included the variables for daily thermoregulatory response, activity status and time of day (Wald $\chi^2 = 475.3, P < 0.001$; Supplementary Data S6). Moose selected wetlands with higher probability during late evening (Fig. 4F) and used wetlands more while active (0.10, 95% CI = 0.05–0.14) than resting (0.05, 95% CI = 0.03–0.07). Furthermore, moose selected wetlands with a slightly higher probability during tolerance days (0.08, 95% CI = 0.04–0.11) than during control days (0.06, 95% CI = 0.03–0.10).

**Microhabitat characteristics of resting sites**

Moose selected resting sites for elevation based on habitat type (Wald $\chi^2 = 2500000.0, P < 0.001$; Supplementary Data S7) by selecting lower areas in wetlands than the surrounding area, while selecting elevated resting sites in all forested habitats (Supplementary Data S8). Additionally, moose selected resting sites for canopy cover based on habitat type within a 5 m (Wald $\chi^2 = 114.3, P < 0.00$; Supplementary Data S7) and 25 m radius (Wald $\chi^2 = 58.46, P < 0.001$; Supplementary Data S7) around the GPS location. Moose chose resting sites with canopy cover that was higher than the surrounding area in all forested habitats (5 m radius cover > 25 m radius cover; Supplementary Data S8). Furthermore, cover at resting sites in late-seral forest was greater than those in mid-seral forest and black spruce forest (Supplementary Data S8).

**Discussion**

Building on the animal indicator concept, our study reveals some of the intricacies between moose physiology and behaviour as these animals navigate the landscape. Non-reproductive female moose in this study exhibited diurnal patterns in the rate of change in rumen temperature, movement rates and drinking during the warm season. Movement rates were greatest in the morning with selection for early-seral forest where forage is abundant. The rate of change in rumen temperature increased at rest when animals typically ruminate and also when movement rates were rapid; however, moderate movement rates were associated with decreasing rate of change in rumen temperatures, which declined rapidly in early-seral forest and during tolerance days in wetlands. During tolerance days, we documented different response curves for the rate of change in moose...
Figure 4: Probability of selection of each habitat type (A–F) by captive adult female moose \((n = 6)\) at the Kenai Moose Research Center on the Kenai Peninsula, Alaska, USA from May through August 2015. Predicted values with 95% confidence intervals from mixed-effect logistic model regression against time of day (0.5 h time periods starting at 0:00) after selecting the best model describing probability of habitat selection for each habitat. Only the top model for early-seral boreal forest (C) included the interaction term between activity status and time of day. Horizontal red dashed line indicates the proportion of the total area each habitat encompassed (e.g. late-seral boreal forest comprised 0.5 or 50% of all vegetation within the study area).

Rumen temperature associated with movement rate when they were in open meadows and in wetlands. We did not detect any shift in the daily pattern for the probability of drinking or the rate of change in rumen temperature in moose during a tolerance day versus a control day. We did detect a difference in moose movement rate during a tolerance day; however, average movement rates increased on tolerance days, which was contrary to our initial hypothesis. In African elephants \((Loxodonta africana)\), movement rate increased with ambient temperature, while using open habitat types, and as they approached water sources \((Thaker et al., 2019)\). Increased movement rates during tolerance days in moose could be a result of direct, quick movements to habitats that provide thermoregulatory relief while reducing the time they remained in open habitats during the day. Furthermore, increased movement rates in this study may also be related to insect avoidance \((Renecker and Hudson, 1990)\); however, we could not detect this type of behaviour response with the data we collected. We also observed a higher rate of increase in the change in rumen temperature when movement rates were high \((\sim > 500 \text{ m} \cdot \text{h}^{-1})\). When planning habitat enhancements or evaluating the effect of natural disturbances, managers should consider the size and shape of habitat patches created on the landscape \((Collins and Schwartz, 1998; Miner, 2000; Wattles and DeStefano, 2013)\). Large blocks of contiguous vegetation patches may increase the distance moose need to travel to access adequate forage or other resources that incur a thermoregulatory cost to the animal.

Similar to other studies on moose, we observed peaks in movement rates during crepuscular periods \((Dussault et al., 2004; Montgomery et al., 2019)\). Montgomery et al. (2019) suggested that shifts to nocturnal activity could compensate for lower activity during the day when ambient conditions are warmer. We propose this change in moose movement rates provides an additional thermoregulatory benefit from foraging. Observed activity rates in these same moose during the summer found 75% of active movement rates were associated with foraging \((Herberg, 2017)\). Furthermore, our study detected decreasing rates of change in rumen temperature during low to moderate movement rates in moose, which we assume are foraging bouts. When ambient conditions are cooler at night, presumably the temperature of the available vegetation on the landscape is also cooler and may become covered in condensation. Foraging on this cool, wet vegetation may allow moose to facilitate the decline in core body temperature to the daily nadir around mid-day \((Thompson et al., 2019)\).

Our study associates behavioural choices of moose with the rate of change in rumen temperature to confirm previous
reports of habitat selection for behavioural thermoregulation in moose (Dussault et al., 2004; Broders et al., 2012; Street et al., 2015; Wattles et al., 2018; Alston et al., 2020; Jenn weave et al., 2020). Open meadow habitats were associated with slightly higher rates of change in rumen temperature on tolerance days; these meadows may have been selected for resting in the early morning when ambient air temperatures were the coolest of all available habitat types (McCann et al., 2016). Furthermore, selection of wetlands increased and resulted in a decrease in the rate of change rumen temperature on tolerance days, with higher selection in the late evening corresponding to higher probabilities of drinking. Resting behaviour by moose in all habitats except wetlands in this study resulted in increasing rumen temperatures. During the summer, moose spend 47–67% of their time bedded, allowing them to rest and ruminate (Renecker and Hudson, 1989; Herberg, 2017). Increases in rumen temperature of resting moose can be attributed to diet-induced thermogenesis and rumination (Lawler and White, 2003; Herberg et al., 2018). We did not detect moose were selecting for specific microhabitats during tolerance days compared to control days; however, we did record moose selected features within each habitat that could provide thermal relief. In forested habitats, moose selected elevated resting sites, which could provide access to wind. Wind can decrease the physiological response of moose to warm ambient conditions (Renecker and Hudson, 1990; McCann et al., 2013) and provide relief from biting insects (Mörschel and Klein, 1997). Additionally, our results show moose selected resting sites in forested habitats with denser canopy cover than the surrounding area to reduce heat loads from solar radiation (Demarchi and Bunnell, 1993; Melin et al., 2014; McCann et al., 2016).

Our study demonstrates behavioural choices of moose on the landscape are associated with the rate of change in rumen temperature and their ability to thermoregulate. Although rumen temperature correlates with core body temperature (Signer et al., 2010; Herberg et al., 2018), inherent biases in rumen temperature are present when animals ingest forage and water. Future studies could use body or vaginal implant temperature loggers to track core body temperature as a response to behaviour. Additionally, using fine-scale accelerometers, magnetometers, and GPS collars could improve behavioural classifications (Hughery et al., 2018) and create dead-reckoned pathways between GPS points (Wens seen et al., 2015) to determine real time habitat use. We suggest future studies on moose response to environmental conditions should incorporate the animal indicator concept (Franzmann, 1983), with body temperature as a physiological indicator of potential heat stress. Individual indices of thermal response advance the classical environmental indicator concept of lower and upper critical temperature thresholds that have been applied to all individuals in all habitats (Renecker and Hudson, 1986; Montgomery et al., 2019; Weiskopf et al., 2019). For large terrestrial herbivores, the animal indicator concept has provided an avenue to understand how trade-offs impact life history characteristics of wildlife populations (Monteith et al., 2013; Bårdsen et al., 2014; White et al., 2014; Long et al., 2016; Middleton et al., 2018). In this study, we applied the animal indicator concept by incorporating the thermal response with continuous core body temperature measurements. Aspects of the landscape of fear (Ditm er et al., 2017, 2018; Oates et al., 2019), including insect harassment (Renecker and Hudson, 1990; Mörschel and Klein, 1997), could also be considered with the animal indicator concept to determine how these factors ultimately influence their life history characteristics with warming temperatures. Ultimately, these trade-offs may be limited by the availability of high-value habitats (Elmore et al., 2017) that could reduce negative effects of warm environmental conditions. Wildlife managers must consider high-value habitats where wildlife can employ both behavioural and physiological mechanisms to tolerate warm ambient conditions in a landscape of forage, predators and pests.

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