Linking forest condition, heat stress, and moose health

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Jeffery Ross Werner
University of Northern British Columbia
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Jeffery R. Werner

EXECUTIVE SUMMARY

Moose (*Alces americanus*) are a cold adapted ungulate whose regional distribution and local abundance are partially determined by sensitivity to heat stress. Moose respond to warm temperatures though changes to behaviour and physiology and will reduce heat load via habitat selection in circumstances where thermal shelter is available. In landscapes where climatic warming and human induced landscape change threatens thermoregulation, it is critical to explicitly define combinations of forest stand characteristics that exacerbate or alleviate thermal stress. I recorded operative temperature (T_e) for one year to describe seasonal pattern and forest characteristics that affect T_e in North-central British Columbia. Significant explanatory variables of T_e varied between the annual time frame and for late winter/early spring, a seasonal period when incidence of thermal stress and frequency of nutritional restriction among collared moose is highest. Multiple linear regression models of mean annual temperature ($R^2 = 0.628$) and frequency of acute hyperthermia ($R^2 = 0.613$) were best explained by a combination of above-ground forest biomass, crown closure, and elevation. Frequency of heat stress was greatest April–May, and a spring regression model ($R^2 = 0.371$) identified biomass as the only significant predictor. Retention of mature productive forest in sufficient amount and evenly distributed over moose range will be necessary to mitigate the accelerating impacts of forest alteration and climatic warming on the thermal environment. Conserving thermal refuge will support individual components of moose fitness such as health, reproduction, and survival consistent with maintaining population management targets and avoiding future population decline.

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INTRODUCTION

Global warming is exerting increased pressure on temperature sensitive wildlife and is expected to cause large-scale changes to ecosystem composition. Throughout the northern hemisphere the effects of these climate trends manifest as phenological mismatch between animal plant and environmental condition, poor demographic performance, and range shifts (Parmesan & Yohe 2003, Roote et al. 2003, Thackeray et al. 2016). Animals can mitigate the adverse impacts heat by altering seasonal or daily activity and by changing habitat selection to favor thermal refuge (Belovsky 1981). On a seasonal scale the biophysical effects of northern forests on local climate are generally shown to have warming effect in winter and cooling in summer, while on daily scales cooling effects predominate during the day and warming during night (Li et al. 2015). Local stand characteristics determine which forest types possess greatest buffering capacity (Demarchi & Bunnell 1993, Ferrez et al. 2011); wildlife are expected to select these habitats during periods where temperature exceeds thermal comfort or induces physiological stress. However, recourse to thermal shelter logically requires that it be in sufficient supply.

The moose is a large cold-adapted boreal ungulate whose present latitudinal range is limited by temperature (Naughton 2012). Owing to its low surface area-to-volume, thick thermally resistant coat, high resting metabolic rate (Hudson & Christopherson 1985), and lack of ability to sweat, moose possess the lowest upper-critical temperature (upper bound of thermal neutral zone) of any northern ungulate (Renecker & Hudson 1986, van Beest et al. 2012). Prolonged thermal stress has been implicated in reduced moose health, reproduction, and survival throughout North America (Murray et al. 2006, Lenarz et al. 2009, DelGiudice et al. 2011, Monteith et al. 2015). Shifting habitat use to older forests that ostensibly provide thermal shelter is an important response moose make to mitigate these adverse conditions (Schwab & Pitt 1991).

In central British Columbia the distribution and abundance of old/mature forest has been greatly reduced and is replaced with young plantations (Dhar et al. 2016) that may not possess the structural properties, nor the thermal mass, necessary to shelter moose during hot and stressful conditions. Where landscape changes driven by commercial forestry yield unexpected consequences for wildlife, it becomes crucial to properly investigate and document these causal

relationships if management practices are to respond favorably through changes in best management, policy guidance, or legislation.

Here, I directly measured operative temperatures (T_e) for an entire year across a wide range of natural and managed forest types and quantified stand characteristics predicted to exacerbate or mitigate thermal stress for a declining moose population. T_e integrates heat transfer from convection, conduction, radiation, and evaporation into a single metric (Bond & Kelly 1955) and provides a more realistic account of the thermal environment an animal is to experience (Dzialowski 2005, Olson et al. 2014). Measured thermal environments and multiple linear regression models of structural forest characteristics were used to predict thermal regimes and frequency of exposure to heat stress in north-central British Columbia. I predicted factors which affect the interception of solar radiation, and the absorption and storage of heat energy would best predict moose exposure to thermal stress, and that these characteristics would be associated with mature and late seral forests.

Study Area

The focal region was the sub-Boreal Spruce (SBS) zone of BC's interior plateau (Figure 1), characterized by a continental climate with cold snowy winters, moderate annual precipitation, and relatively short, warm and moist summers (Meidinger & Pojar 1991). Most of the zone is covered with coniferous forests. Subalpine fir (*Abies lasiocarpa*) and hybrid white spruce (*Picea engelmannii x glauca*) and are the dominant species in mature and old forests. Younger forests are dominated by lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Black spruce (*Picea mariana*) is limited to wetter sites and balsam popular (*Populus balsamifera*) to riparian and alluvial deposits. Douglas-fir (*Pseudotsuga menziesii*) is scattered but abundant in warm and dry primary (uncut) forests, and veteran trees comprise important litter forage for moose (Rae et al. 2014). Industrial forest harvest followed by predominantly monoculture plantations have created an overabundance of early seral even-aged pine dominated forest.

Mean monthly temperatures in the vicinity of Prince George range from a low of -7.5°C in January to a high of 16.5°C in July, with an annual mean temperature of 2.2°C. First snowfall

usually occurs in late October and final snowfall in early April. Mean annual precipitation is 636 mm with nearly 40% of that falling as snow (Moore et al. 2010).

METHODS

To measure T_e across the region I identified sites with a significant range of forest ages, site indices, height, structural biomass, harvestable volume, canopy closure, and stem density using the BC government Vegetation Resources Inventory (VRI). VRI partitions the landscape into polygons with similar stand characteristics using a combination of photo interpretation and ground sampling (permanent mensuration sample plots) covering most public lands in the Province (BC Gov 2021). Using the centroid of each polygon as the reference point, I obtained aspect, slope, and elevation from a provincial digital elevation model (DEM 1:20 000 scale) using a GIS.

Construction of Operative Temperature Recorders

Black body temperature stations comprised one data-logging thermocouple (iButton DS1922L 8KB memory) suspended within a sealed air-tight copper toilet tank float (11 x 11 x 13 cm; 70g) painted matt black. Loggers were synchronized to record temperature (accurate to $\pm 0.5°C$) every 1.25 hours continuously for an entire year (August 1, 2019 –July 31, 2020). The length of time between recording events was determined by the memory capacity of the logger.

Logger Deployment

Loggers were positioned at the centroid of each VRI study polygon. Exact locations were identified in the field using a handheld GPS (accurate to ±3m) to identify the nearest windfirm tree to the centroid's coordinates. At each location operative temperature stations were fixed 1.5 m above ground surface and 1m from the truck of the installation tree (figure 2) by hanging the globe off the end of a 1.2m long wooden piece of spruce lathe with 12-gauge copper wire (Figure 2). I hung each globe on the north side of the installation tree (following Olsen et al. 2014). Black globes were deployed July 15-28, 2019 (programed to start recording August 1, 2019) and retrieved August 1-August 8, 2020 (programed to stop recording July 31, 2020. To avoid the complicating micro-climatic effects of edge, loggers were placed >120m from a forest edge.

Stress thresholds

There exist competing claims over which season-specific temperature thresholds best predict moose thermal stress (Table 1). This controversy is the result of different authors using different reporting units and/or measurement methods. While some authors describe the impact of ambient temperature (T_a) others either model or directly measure operative temperature (T_e). Renecker & Hudson (1986) reported onset of heat stress (exceeding the upper critical limit resulting in increased metabolism) during winter at -5°C and acute stress (visible panting) at 0°C. They also reported onset of stress during summer at 14°C and acute stress at 20°C. These two lower threshold temperature values (0°C and 14°C) have become synonymous with the upper critical temperature for moose (Broders et al. 2012, van Beest et al. 2012). For purposes of this study I model and report the more precautious upper values (0°C and 20°C) associated with acute stress (Renecker & Hudson 1986, 1990).

However, Renecker & Hudson (1986) do not report thresholds for spring and autumn seasons. To obtain a continuous year-round series of seasonal thresholds, I modelled the onset of acute stress for spring and autumn using linear daily transitions between summer and winter. The four seasons are defined based on observations of molt reported by Thompson et al. (2020) (Figure 3). Specifically, moose were assumed to have a winter coat November 1 – May 1 (winter), molt May 1 – July 1 (spring), maintain a summer coat July 1 – September 1 (summer), and exhibit winter coat growth September 1 – November 1 (autumn). To quantify frequency of acute heat stress, each operative temperature recording was scored as being under or over the daily modelled threshold.

Habitat variables

Prior to statistical analyses, the repertoire of independent variables extractable from the VRI and the DEM were scrutinized for their ability to contribute to an understanding of causal mechanisms. Site index, age, stand height, and harvestable volume were dropped in favor above-ground biomass (stems, branches, bark, and foliage of live trees and any dead material) because biomass has direct relevance to thermal mass and because the dropped variables contribute directly to calculation of biomass. After analyses were complete a strong positive correlation between stand age and biomass was discovered (r^2=0.86) which lent support to the decision to

drop age in favor of biomass. Canopy closure (%) was included because it affects the rate of interception of solar radiation and because of its use in prior studies of thermal refuge (e.g. Demarchi & Bunnell 1995). Cumulative stem length, calculated as stem density per ha of dominant and subdominant trees multiplied by their estimated heights (m), was retained because it reflects the distribution of the biomass (several large vs many small) not accounted for in total biomass. Aspect and slope were removed from the list of explanatory variables after the DEM model outputs indicated that study sites were relatively flat. (<5% slope). Elevation was retained because the adiabatic lapse rate predicts the temperature of a parcel of air will decrease with increase in altitude (Stone & Carlson 1979).

Statistical Analysis

Multiple linear regression models were run in NCSS (NCSS 2021) statistics software to determine the value of each independent continuous variable as a model predictor for three separate response variables: mean annual operative temperature (MAT_e), annual frequency of acute heat stress, and spring (April–May) frequency of acute stress. The choice to model acute thermal stress during spring was made after graphical inspection revealed this period to be almost exclusively outside of the thermal neutral zone. To assess degree of variability in operative between habitat types I calculated coefficient of variation (CV) for each temperature logger after first having converted T_e to degrees kelvin to remove problematic negative values. Absolute range (annual min minus max) was calculated as an additional index of variation.

I used residual plots to assess the distribution of the three response variables and to clarify if model assumptions were met. Outputs of regression analyses for independent variables include estimate, standard error (SE) and p-value. Ratio of independent variables to overall sample size was small (>10 subjects per predictor) and risk of overfitting was therefore deemed to be low.

To assess goodness of fit of each global model, coefficients of multiple determination (R-squared; R^2) are reported. Residual plots were first examined for bias prior to calculating R^2 and bias in the distribution of residuals were not indicated. Summary statistics were computed for the response and independent variables, including means, medians, standard deviation, minimum values, maximum values, and the interquartile range. Means are reported in text accompanied by ± SE, and an α of 0.05 was used to assess significance throughout. For single regressions (one

independent variable) I used the linear regression t-test to determine if the slope of the regression line differed significantly from zero.

To assess for bias associated with a single year of study yielding either unseasonably warm or uncharacteristically cool weather patterns I compared the monthly ambient air temperatures for teach month the loggers were deployed (August 1 2019 – July 31 2020) with the long-term monthly average (1943 – 2020) from the Prince George airport weather station.

Of the 102 T_e loggers deployed during 2019, 66 were retrieved undamaged. Of the 36 black globes that were damaged, 5 failed, 11 were on the ground with punctures indentations consistent with being chewed by bears, and 20 contained bullet holes. Damaged loggers were removed from analysis.

The regional mean annual temperature (all loggers combined) was 5.08 ± 0.13°C (range=3.19-7.80) August 2019–July 2020 (Table 2). On average 33.8 ± 0.70% of all T_e recorded during this time exceeded the upper limit of acute thermal stress. Including all instances where operative temperature exceeded the upper limit of thermal neutrality (lower threshold) increased this proportion to 66.5 ± 0.34%. During early spring (April–May 2020) the mean proportion of acute thermal stress was 77 ± 0.51% (Table 2) and the mean proportion of any thermal stress (lower threshold) was 91.2 ± 0.32%. Visual inspection of histograms confirmed the distribution of mean temperatures and the frequencies of heat stress were approximately symmetric, did not violate the normality assumption and hence, that the chosen regression models were appropriate.

The mean age of dominant trees within the study sites was 88.32 ± 7.96 years (range 3 – 305), with mean crown closure of 39.87 ± 2.86 % (range 1 – 87), mean cumulative stem length of 15941 ± 1605.01 m/ha (range 326 – 55800), mean above ground biomass of 148.72 ± 12.82 m^3/ha (range 0.2 – 366), and mean elevation of 767.0 ± 11.02 m asl (range 570 – 902) (Table 3).

Thermal Stress frequency and timing

The annual pattern of thermal neutrality, initial heat stress, and of acute hyperthermic conditions varied by site but showed consistent patterns between months regardless of site (Figure 4a-b). Specifically, all habitats exhibited the lowest proportion of thermal neutrality and highest proportion of thermal discomfort (low and high thresholds combined) during April (T_e > lower threshold 85% of the time) and May (98%). Those months with the third and fourth most frequent exceedances of the upper critical limit of neutrality were October (~77%) and November (75%), respectively (Figure 7).

Habitat drivers

Crown closure (p=0.012), above-ground biomass (p<0.0001) and elevation (p<0.0001) were significant predictors of mean annual operative temperature (Table 4). Cumulative stem length was not a significant variable. The multiple regression model with these four predictors accounted for nearly 63% of the variance in mean annual temperature. The estimates for each of the significant predictors were negative, indicating that an increase in crown closure, biomass, or elevation is expected to yield a decrease in the mean annual operative temperature (Table 4).

Crown closure (p=0.0095) and above ground biomass (p<0.0001) are identified as attributes that have a significant effect on the proportion of temperature recordings exceeding the upper critical threshold for acute thermal stress (Table 5). In the case of both predictors, the estimates are negative indicating that increased crown closure or biomass is expected to yield a decrease in proportion of thermal stress experienced at that location. The full model containing closure, biomass, length, and elevation accounted for 61% of the variance in upper thermal stress threshold exceedances (Table 5).

Above ground biomass (p<0.0001) was identified as the only significant variable predicting amount of acute thermal stress experienced by moose during April–May (Table 6). The full model containing all four predictors accounted for 37% of the variance in the frequency of acute heat stress and the value of the estimate indicates that increasing forest biomass is expected to yield a decline in exposure to acute thermal stress (Table 6).

In addition to being the only significant variable in common to each model, biomass exhibited a high degree of correlation with the annual coefficient of variation of mean annual operative temperature ($r^2 = 0.62$, $t(61) = -9.734$, $p<0.0001$) and with the range of operative temperatures recorded for each location ($r^2 = 0.48$, $t(61) = -7.254$, $p<0.0001$) (Figure 5).

The year of study in context

Comparison of mean monthly temperatures for the period of study with the long-term (77 year) average from the Prince George airport indicated that trends for the study period were generally consistent and fell within the one standard deviation of the long-term mean 10 months out of 12

(Figure 6). The mean monthly temperatures from October 2019 and from March 2020 were slightly lower than the historic average.

DISCUSSION

Owing to their size and thick coat, moose incur greater energetic costs with increasing temperature than other ungulates, but specific thresholds at which individuals experience stress will vary with solar exposure, humidity, and wind speed (Parker & Gillingham 1990). Studies relating moose physiology or behavior to ambient temperature that do not take these additional factors into account may contribute needless debate about which specific temperature thresholds are likely to induce stress (McCann et al. 2013, Mitchell et al. 2018, Montgomery et al. 2019).

Renecker and Hudson (1986) determined upper critical temperatures by measuring respiration rates of non-reproductive fasting moose under controlled conditions. They identified 14 °C as triggering hyperventilation and increased metabolism, and 20 °C when moose began open mouth panting during summer; analogous thresholds of -5 °C and 0 °C were reported for winter. Under controlled environments the confounding influence of wind, moisture, and sunlight are reasonably diminished and estimates of T_a begin to approach T_e. However, to understand thermal influence on free-ranging wildlife in diverse landscapes, we benefit from integrating all modes of heat transfer into a single metric as well as distinguishing critical temperatures for all seasons.

Here I report habitat-specific mean annual operative temperature and seasonal frequency of acute hyperthermia from a wide variety of forested habitats of central British Columbia. By combining empirical measures of black body temperature for an entire year with daily modelled thresholds of thermal stress, we conclude that moose likely experience substantial thermal challenge in all seasons with April and May potentially being the most acute, followed by October and November. This appears to be among the first studies to highlight spring and autumn as the most vulnerable season periods (but see Schwab & Pitt 1991).

Thermal refuge was greatest in older stands containing large mature trees, and well-developed crowns with higher and multi-layered canopy closure. Estimates of biomass, canopy closure and elevation, which were readily available from forest inventory datasets, performed reasonably well in explaining variation in thermal environments from a variety of forested stand types. That the spring stress regression model contained fewer significant habitat variables and performed less well ($R^2 = 0.37$ vs $R^2 = 0.61$–0.63) suggests that the moderating influence of thermal mass

on operative temperature may be less, perhaps owing to the transition from winter to snow-free (April) and frost-free (May) conditions. Unlike others who have investigated seasonal temperature differences between broad forest types (e.g., mixed forest vs coniferous forest; McGraw et al. 2012), I used measurable stand characteristic believed to influence thermal mass and energy exchange across the full range of forest ages in north-central BC.

Both Demarchi & Bunnell (1995) and Van Beest et al. (2012) have shown that summer habitat uses shift towards mature dense-canopied forest as temperatures rise, suggesting that moose trade abundant open-grown forage for cover during periods of thermal stress. Street et al. (2015) reported that moose increased selection for stand height (a potential index of biomass) during warmer periods. Shifts in habitat use are often more acute during summer than winter (Dussault et al. 2004, Van Beest et al. 2012), which is consistent with other studies who report temperature-mediated behavior during the snow-free season (Melin et al. 2014).

Lenarz et al. (2009) found that moose survival in subsequent seasons could be predicted from the frequency of late-winter and early-spring temperatures that exceed the upper critical temperatures (lower threshold) reported by Renecker & Hudson (1986). Moose increase their metabolic rate to regulate their core temperature which may affect behavioral tradeoffs between energy acquisition and safety (McNamara & Houston 1992, 1996), and cumulatively influence energy reserves (Shively et al. 2019), chronic stress (Spong et al. 2020) and other indices of health (McCann et al. 2013), reproduction (Monteith et al. 2015, Ruprecht et al. 2016), and survival (Lenarz et al. 2009).

However, several important questions remain, including what role the availability of aquatic, aspect-dependent, and micro-climatic habitats may play for moose seeking shelter from heat (Telfer 1988, Olsen et al. 2014, McCann et al. 2016). The strength of influence that these factors exert on thermal refuge varies with season (Olsen et al. 2014); examining their role for moose will require further investigation and multiple years of T_e data from a wide variety of forested habitats. Widespread recognition of the importance of T_e has resulted in attempts to incorporate indices of heat stress into habitat suitability models (Haase & Underwood 2013).

In north-central BC, poor health among collared moose cows is an emerging issue (Proctor et al. 2020) implicated in a substantial fraction of known mortality events. Local moose populations have also declined by ~70% since the early 2000's (Werner 2020). Although the cause(s) of

these population reductions are not yet resolved, the timing of population decline was concurrent with widespread salvage logging in the wake of a pine beetle outbreak. Approximately half of recent (2012-2020) collared cows whose deaths were investigated were found to be in poor (22%) body condition or in a state of acute malnutrition (30%) (Proctor et al. 2020). The chief cause of mortality among acutely malnourished cows was apparent starvation. Most mortalities of adult cows in poor body condition occurred between April and June (Proctor et al. 2020), which approximately corresponds to the window of most severe heat stress reported here.

Widespread conversion of mature primary forest to early-seral plantation has reduced the regional supply of thermal refuge for at least one temperature-sensitive ungulate. Climatic warming coupled with loss of thermal shelter can adversely affect moose populations, especially in instances where forage quality is marginal (Shively et al. 2019) as has been shown in late summer (McArt et al. 20) and in some managed landscapes (Happe et al. 1990, Werner & Parker *in prep*). Thermal tolerance of moose to climate change will depend on the duration and intensity of exposure to acute thermal stress and the ability of the animal to dissipate heat load using physiological and behavioral responses that may require access to high quality thermal refuge.

LITERATURE CITED

Barboza, P.S., K.L. Parker, &Hume, I.D. 2009. Integrative Wildlife Nutrition. Volume 1. Springer-Verlag, Berlin Heidelberg.

BC Gov. 2020. Vegetation Resources Inventory. https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-inventory/data-management-and-access/vri-data-standards. Accessed November 13, 2020 from https://data.gov.bc.ca/.

Belovsky, G.E. 1981. Optimal activity times and habitat choice of moose. Oecologia, 48(1), 22-30.

Bond, T.E., & Kelly, C.F. 1955. The globe thermometer in agricultural research. Agricultural Engineering 36: 251.

Broders, H.G., Coombs, A.B., & McCarron, J.R. 2012. Ecothermic responses of moose (Alces alces) to thermoregulatory stress on mainland Nova Scotia. Alces: A Journal Devoted to the Biology and Management of Moose, 48, 53-61.

DelGiudice, G.D., Sampson, B.A., Lenarz, M.S., Schrage, M.W., & Edwards, A.J. 2011. Winter body condition of moose (Alces alces) in a declining population in northeastern Minnesota. Journal of Wildlife Diseases, 47(1), 30-40.

Demarchi, M.W., & Bunnell, F.L. 1993. Estimating forest canopy effects on summer thermal cover for Cervidae (deer family). Canadian Journal of Forest Research, 23(11), 2419-2426.

Demarchi, M.W., & Bunnell, F.L. 1995. Forest cover selection and activity of cow moose in summer. Acta Theriologica, 40(1), 23-36.

Dhar, A., Parrott, L., & Hawkins, C.D. 2016. Aftermath of mountain pine beetle outbreak in British Columbia: Stand dynamics, management response and ecosystem resilience. Forests, 7(8), 171.

Dussault, C., Ouellet, J.P., Courtois, R., Huot, J., Breton, L., & Larochelle, J. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience, 11(3), 321-328.

Dzialowski, E.M. 2005. Use of operative temperature and standard operative temperature models in thermal biology. Journal of Thermal Biology, 30(4), 317-334.

Ferrez, J., Davison, A.C., & Rebetez, M. 2011. Extreme temperature analysis under forest cover compared to an open field. Agricultural and Forest Meteorology, 151(7), 992-1001.

Haase, C.G., & Underwood, H.B. 2013. Integrating thermal constraints into habitat suitability for moose in the Adirondack State Park, New York. Alces: A Journal Devoted to the Biology and Management of Moose, 49, 49-64.

Happe, P.J., Jenkins, K.J., Starkey, E.E., & Sharrow, S.H. 1990. Nutritional quality and tannin astringency of browse in clear-cuts and old-growth forests. The Journal of wildlife management, 557-566.

Hudson, R.J., & Christopherson, R.J. 1985. Maintenance metabolism. In: Hudson, R.J. & White, R.G. (Eds). Bioenergetics of wild herbivores. CRC Press, Boca Raton, 121-142.

Lenarz, M.S., Nelson, M.E., Schrage, M.W., & Edwards, A.J. 2009. Temperature mediated moose survival in northeastern Minnesota. The Journal of Wildlife Management, 73(4), 503-510.

Li, Y., Zhao, M., Motesharrei, S., Mu, Q., Kalnay, E., & Li, S. 2015. Local cooling and warming effects of forests based on satellite observations. Nature communications, 6(1), 1-8.

McArt, S.H., Spalinger, D.E., Collins, W.B., Schoen, E.R., Stevenson, T., & Bucho, M. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology, 90(5), 1400-1411.

McCann, N.P., Moen, R.A., & Harris, T.R. 2013. Warm-season heat stress in moose (Alces alces). Canadian Journal of Zoology, 91(12), 893-898.

McCann, N.P., Moen, R.A., Windels, S.K., & Harris, T.R. 2016. Bed sites as thermal refuges for a cold-adapted ungulate in summer. Wildlife Biology, 22(5), 228-237.

McNamara, J.M., & Houston, A.I. 1992. Risk-sensitive foraging: a review of the theory. Bulletin of mathematical biology, 54(2-3), 355-378.

McNamara, J.M., & Houston, A.I. 1996. State-dependent life histories. Nature, 380(6571), 215-221.

McGraw, A.M., Moen, R.A., & Overland, L.G. 2012. Effective temperature differences among cover types in northeast Minnesota. Alces: A Journal Devoted to the Biology and Management of Moose, 48, 45-52.

Meidinger, D., & Pojar, J. 1991. Ecosystems of British Columbia. Special Report Series-Ministry of Forests. British Columbia, (6). https://www.for.gov.bc.ca/hfd/pubs/Docs/Srs/Srs06.htm

Melin, M., Matala, J., Mehtätalo, L., Tiilikainen, R., Tikkanen, O.P., Maltamo, M., ... & Packalen, P. 2014. Moose (Alces alces) reacts to high summer temperatures by utilizing thermal shelters in boreal forests–an analysis based on airborne laser scanning of the canopy structure at moose locations. Global Change Biology, 20(4), 1115-1125.

Mitchell, D., Snelling, E.P., Hetem, R.S., Maloney, S.K., Strauss, W.M., & Fuller, A. 2018. Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. Journal of Animal Ecology, 87(4), 956-973.

Monteith, K.L., Klaver, R.W., Hersey, K.R., Holland, A.A., Thomas, T.P., & Kauffman, M.J. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. Oecologia, 178(4), 1137-1148.

Montgomery, R.A., Redilla, K.M., Moll, R.J., Van Moorter, B., Rolandsen, C.M., Millspaugh, J. J., & Solberg, E.J. 2019. Movement modeling reveals the complex nature of the response of moose to ambient temperatures during summer. Journal of Mammalogy, 100(1), 169-177.

Moore, R.D., Spittlehouse, D.L., Whitefield, P.H., & Stahl, K. Weather and Climate. In: Pike, R. G., Redding, T. E., Moore, R. D., Winkler, R. D., & Bladon, K. D. 2010. Compendium of forest hydrology and geomorphology in British Columbia. Land Management Handbook-Ministry of Forests and Range, British Columbia, (66).

Murray, D. L., Cox, E.W., Ballard, W.B., Whitlaw, H.A., Lenarz, M.S., Custer, T.W., ... & Fuller, T.K. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs, 166(1), 1-30.

Naughton, D. 2012. The natural history of Canadian mammals. University of Toronto Press.

NCSS 2021 Statistical Software (2021). NCSS, LLC. Kaysville, Utah, USA, ncss.com/software/ncss.

Olson, B., Windels, S. K., Fulton, M., & Moen, R. 2014. Fine-scale temperature patterns in the southern boreal forest: implications for the cold-adapted moose. Alces: A Journal Devoted to the Biology and Management of Moose, 50, 105-120.

Parmesan, C., & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421(6918), 37-42.

Procter, C., M. Anderson, M. Schiedeman, S. Marshall, H. Schindler, H. Schwantje, D. Hodder, and E. Blythe. 2020. Factors affecting moose population declines in British Columbia. 2019 Progress Report: February 2012–May 2020. B.C. Min. For., Lands, Nat. Resour. Ops. and Rural Dev. Victoria, B.C. Wildl. Working Rep. WR-128.

Renecker, L.A., & Hudson, R.J. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology, 64(2), 322-327.

Renecker, L.A., & Hudson, R.J. 1992. Thermoregulatory and behavioral response of moose: is large body size an adaptation or constraint. Alces Supplement, 1(52.64).

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., & Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. Nature, 421(6918), 57-60.

Ruprecht, J.S., Hersey, K.R., Hafen, K., Monteith, K.L., DeCesare, N.J., Kauffman, M.J., & MacNulty, D.R. 2016. Reproduction in moose at their southern range limit. Journal of Mammalogy, 97(5), 1355-1365.

Shively, R.D., Crouse, J.A., Thompson, D.P., & Barboza, P.S. 2019. Is summer food intake a limiting factor for boreal browsers? Diet, temperature, and reproduction as drivers of consumption in female moose. PloS one, 14(10), e0223617.

Schwab, F.E., & Pitt, M.D. 1991. Moose selection of canopy cover types related to operative temperature, forage, and snow depth. Canadian Journal of Zoology, 69(12), 3071-3077.

Spong, G., Gould, N.P., Sahlén, E., Cromsigt, J.P., Kindberg, J., & DePerno, C.S. 2020. Large-scale spatial variation of chronic stress signals in moose. Plos one, 15(1), e0225990.

Street, G.M., Rodgers, A.R., & Fryxell, J.M. 2015. Mid-day temperature variation influences seasonal habitat selection by moose. The Journal of Wildlife Management, 79(3), 505-512.

Stone, P.H., & Carlson, J.H. 1979. Atmospheric lapse rate regimes and their parameterization. Journal of Atmospheric Sciences, 36(3), 415-423.

Telfer, E.S. 1988. Habitat use by moose in southwestern Alberta. Alces, (24), 14.

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., ... & Wanless, S. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature, 535(7611), 241-245.

Thompson, D.P., Barboza, P.S., Crouse, J.A., McDonough, T.J., Badajos, O.H., & Herberg, A.M. 2019. Body temperature patterns vary with day, season, and body condition of moose (Alces alces). Journal of Mammalogy, 100(5), 1466-1478.

Thompson, D.P., Crouse, J.A., Jaques, S., & Barboza, P.S. 2020. Redefining physiological responses of moose (Alces alces) to warm environmental conditions. Journal of Thermal Biology, 90, 102581.

Werner, J.R. 2020. Moose Population Reconstruction for the PG West Area. Draft Technical Analyses. Internal Report. June 10, 2020. 23pp.

Werner, J.R. & Anderson, M. 2017. An approach to investigate 'apparent starvation' in moose populations: a preliminary scoping. Ministry of Forests, Lands, and Natural Resource Operations. Omineca region. 19pp.
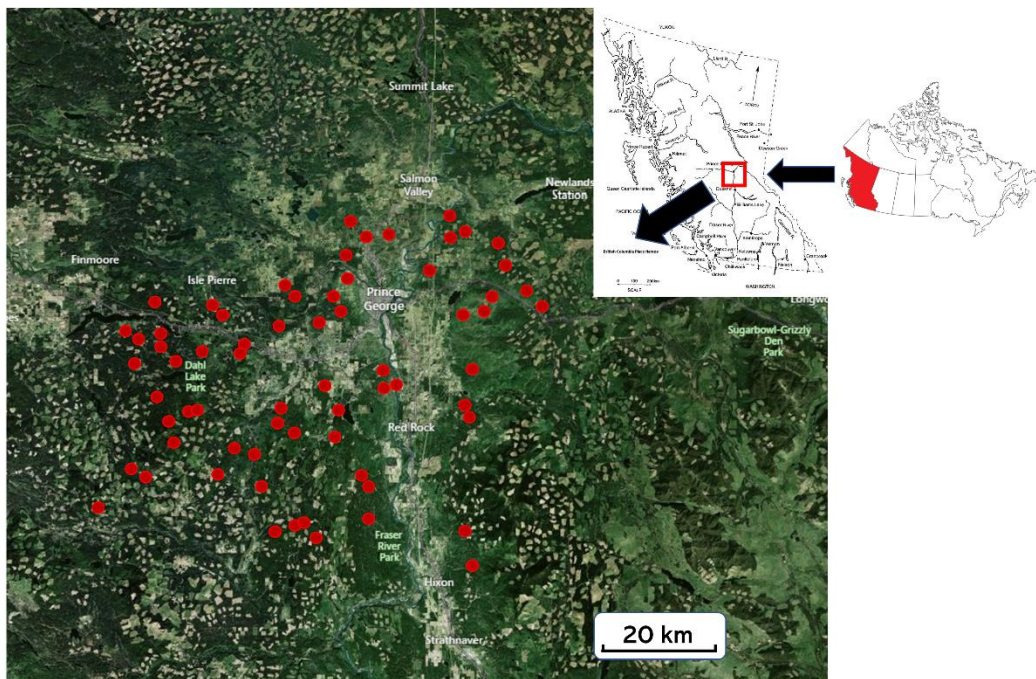
Figure 1: Approximate locations of black body operative temperature (T_e) logging stations in North-central BC, August 1, 2019—July 31, 2020.

Figure 2: Black body operative temperature (T_e) logger installed in a 42-year-old spruce stand, north-central BC.
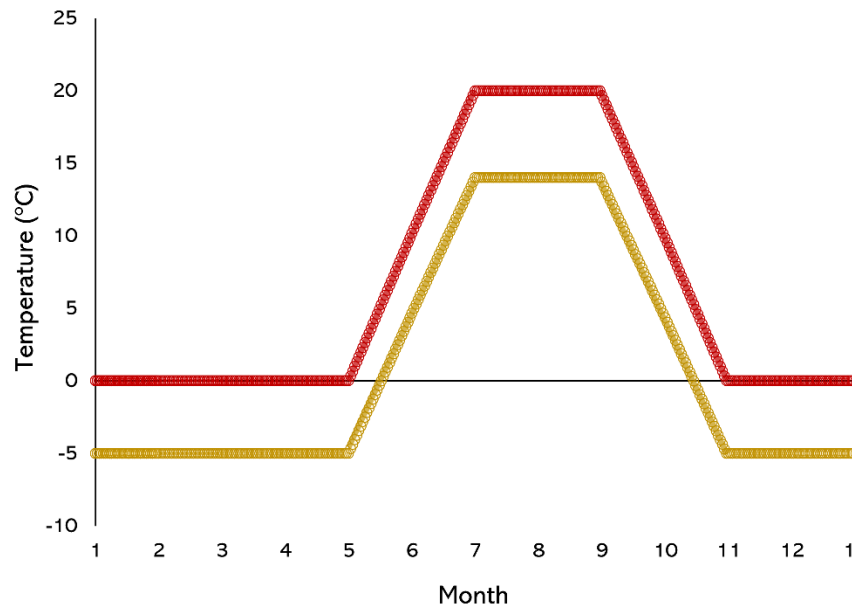
Figure 3: Upper critical temperature (yellow) of the thermoneutral zone, and the onset of acute stress (red) for moose north-central British Columbia, Canada. Moose are assumed to have a winter coat November 1—May 1, molt May 1—July 1, summer coat July 1—September 1, and exhibit winter coat growth September 1—November 1 (Thompson et al. 2020). Upper acute [lower onset] heat stress in summer = 20 °C [14 °C] and winter 0 °C [-5 °C] as defined by Renecker and Hudson (1986). Transitions between summer and winter thresholds are modelled as linear functions.
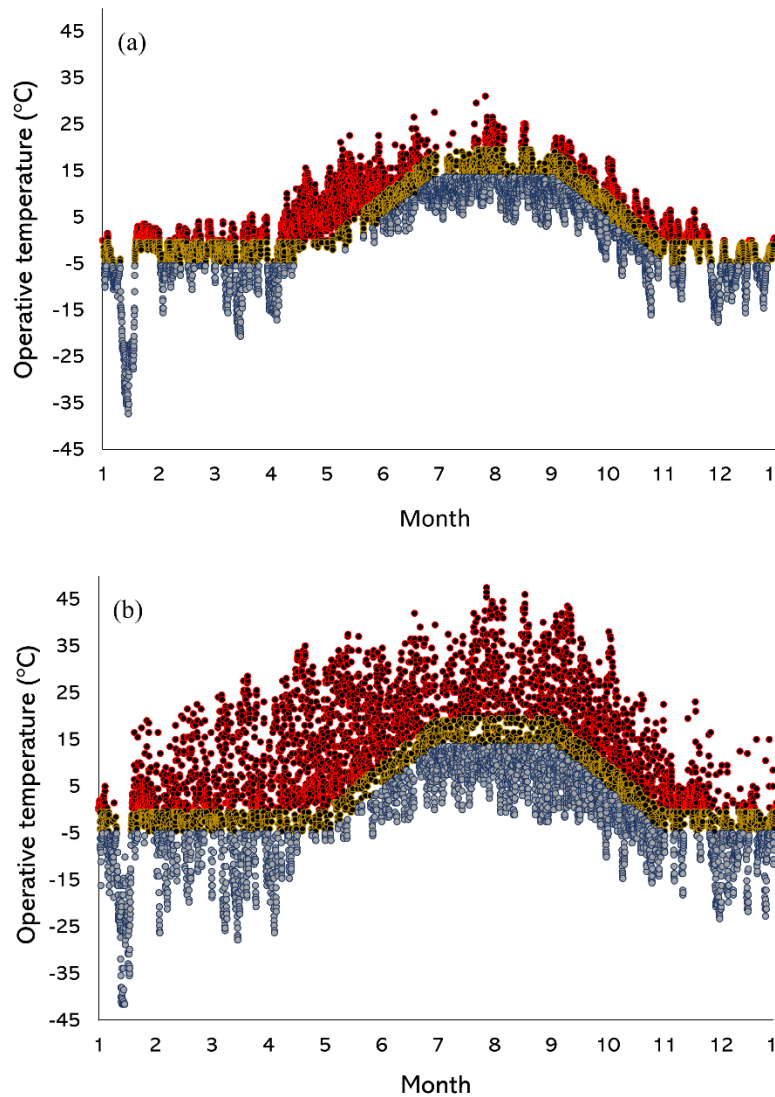
Figures 4a-b: Examples of operative temperature (T_e) recordings partitioned into thermal neutral (blue) early onset of thermal challenge (above upper critical temperature but below acute stress; yellow), and acute thermal stress (hyperthermia; red), with linear transitions linking summer and winter thresholds reported by Renecker & Hudson (1986). Data are for (a) mature (170 year) spruce-leading stand and (b) plantation containing 15-year-old spruce-leading planted stock, within BC's Sub-boreal spruce Biogeoclimatic subzone (SBD dw3). Note that the months of April and May contain the fewest incidence of thermally neutral (no stress) conditions for moose.
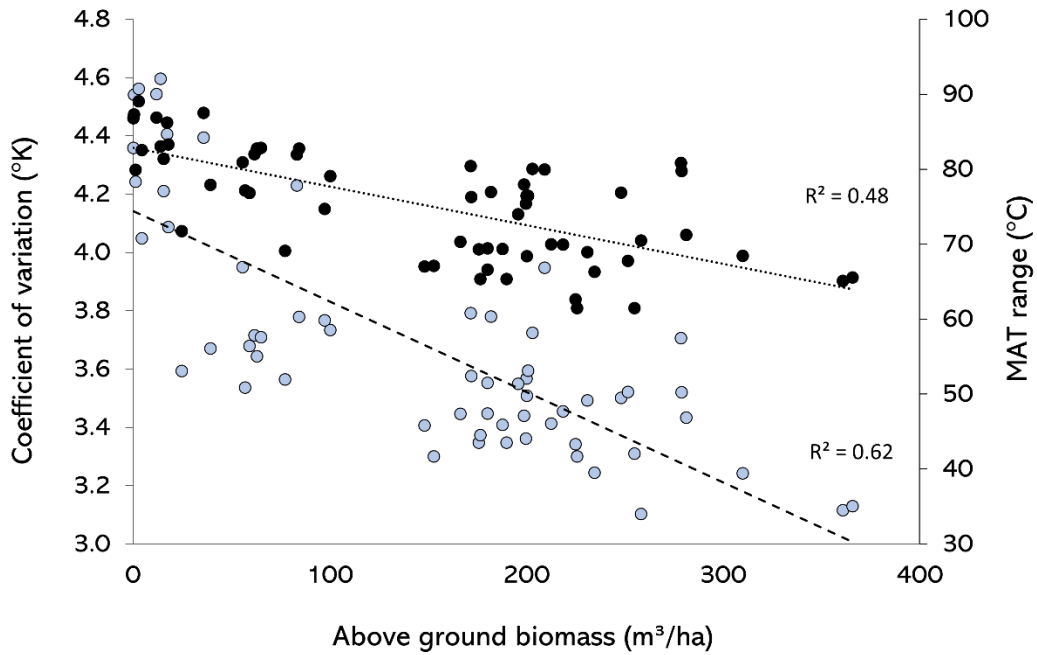
Figure 5: The variation in mean annual operative temperatures as a function of above ground forest biomass, expressed as coefficient of variation (grey circles; converted kelvin) and absolute range (black circles; maximum temperature subtracted by minimum). Data from the sub-boreal spruce biogeoclimatic zone, north-central BC.
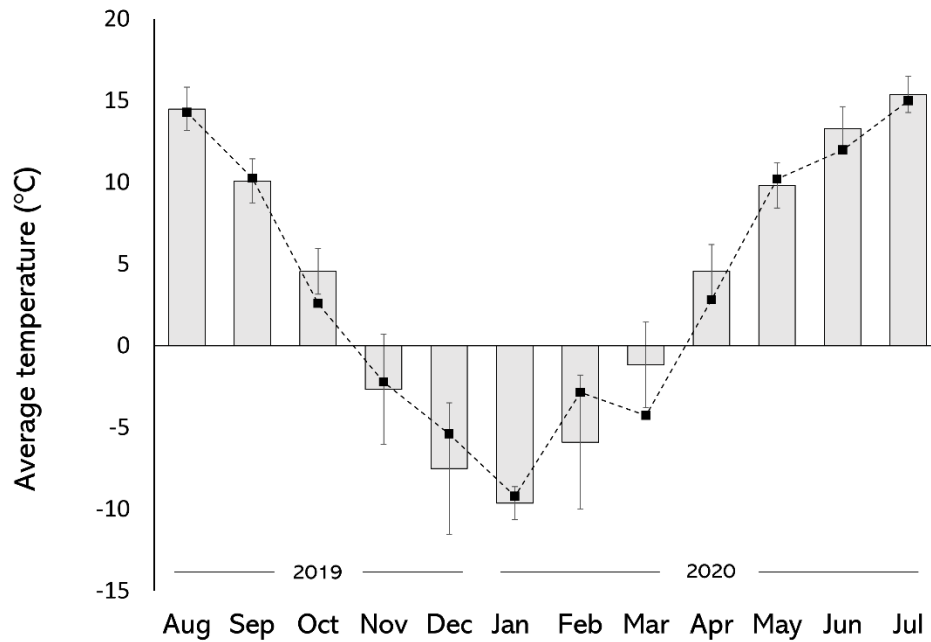
Figure 6: Mean monthly temperature for the study (August 1, 2019 – July 31, 2020) (black squares) and the long term mean monthly average (1943-2020) (shaded bars) for the Prince George airport permanent weather station (bars are for long-term ±SD for the long-term data). Monthly temperatures during the period of study were generally consistent with the long-term average, being slightly cooler during October, March, and April, and slightly warmer during December and February.
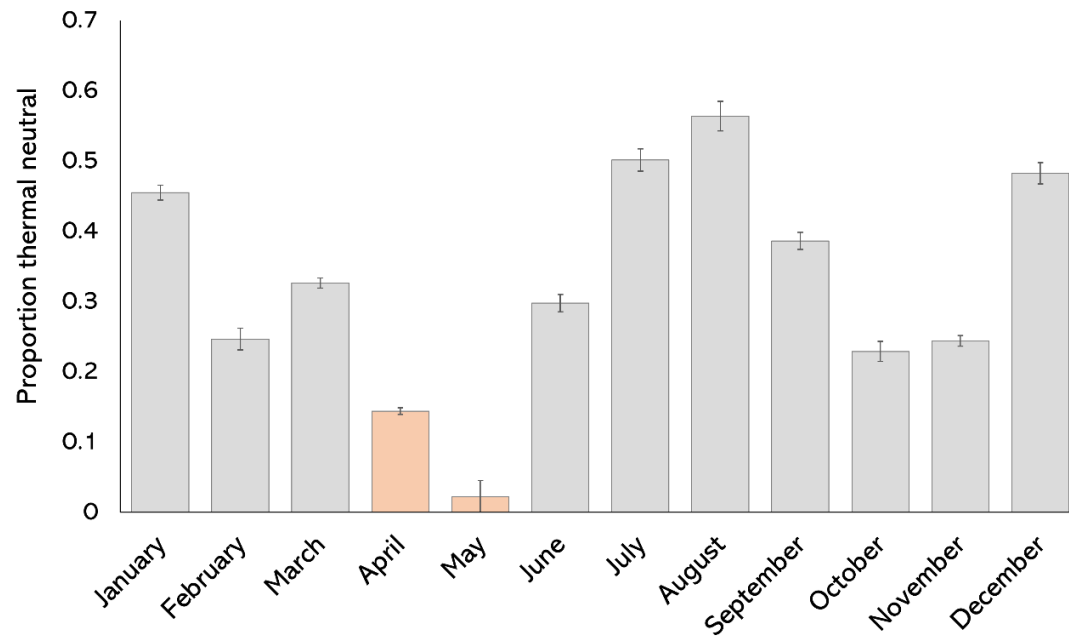
Figure 7: Proportion of monthly operative temperatures (T_e) within the moose thermal neutral zone. April and May (orange bars) have the greatest risk of thermal stress. Bars are 95% confidence intervals. Data collected August 1, 2019 through July 31, 2020; SBS biogeoclimatic zone, north-central BC.

Table 1: Various temperature thresholds for moose stress recorded in the literature. Discrepancies are likely because some authors measure ambient temperature (T_a) while others measure operative temperature (T_e).

Season	Temp °C	Comment	Reference
Summer	14	The low upper critical temp during calm conditions; increased metabolism, heart rate, respiration rate; reduced feeding rate & weight gain	Renecker & Hudson 1986
	17	Low upper critical temp under windy conditions	McCann et al. 2013
	20	Upper critical temp; associated with open-mouthed panting to regulate core body temperature	Renecker & Hudson 1986
	24	Upper critical temp when bedded under windy conditions	Renecker & Hudson 1986
Winter	>-5	Increased respiration	Renecker & Hudson 1986; Schwartz & Renecker (2007)
	0	Upper critical temp; associated with open-mouthed panting to regulate core body temperature	Renecker & Hudson 1986

Table 2: Summary statistics for response variables of mean annual operative temperature (MAT$_e$), and the annual and spring frequency of acute thermal stress.

Variable	Mean	Median	Standard Deviation	Inter-quartile range	Minimum	Maximum
MAT	5.08	4.87	0.99	1.37	3.19	7.80
Annual frequency	0.34	0.33	0.05	0.08	0.25	0.45
Spring frequency	0.77	0.77	0.04	0.03	0.61	0.82

Table 3: Summary statistics for the independent predictor variables of crown closure (%), cumulative stem length (m/ha), above ground biomass of live and dead material (m^3/ha), and elevation (m asl) used to predict mean annual operative temperature, the annual frequency of heat stress, and the seasonal spring frequency of heat stress.

Variable	Mean	Median	Standard Deviation	Inter-quartile range	Minimum	Maximum
Closure	39.87	45.00	22.13	40.00	1.00	87.00
Length	15941.00	13704.00	12439.93	11644.50	326	55800
Biomass	148.72	176.30	99.32	155.48	0.20	366.00
Elevation	767.00	794.01	85.33	130.75	570.0	902.0

Table 4: Results of multiple linear regression analyses of habitat variables on mean annual temperature (MAT$_e$).

Coefficient	Zero-order r	Estimate (β)	Standard error	P-value
Closure	-0.47	-0.01	0.004	0.012
Biomass	-0.64	-0.006	0.0009	0.00000003
Length	-0.22	0.000009	0.000008	0.257
Elevation	-0.40	-0.005	0.001	0.0000002

Global adjusted model R^2 = 0.628

Table 5: Results of multiple linear regression analyses of habitat variables on the annual frequency of acute heat stress for moose (August 1, 2019-July 31, 2020) using operative temperature (T_e). Upper critical temperature in summer (20°C) and Winter (0°C) as defined by Renecker & Hudson (1986) and daily linear transitions for spring and autumn seasons as defined by Thompson et al. (2020). Moose assumed to have a winter coat from November 1 through May 1, molt from May 1 to July 1, summer coat from July 1 to September 1, and winter coat growth from September 1 to November 1. Data from the Omineca region, North-central BC, Canada.

Coefficient	Zero-order r	Estimate (β)	Standard error	P-value
Closure	-0.53	-0.00063	0.0002	0.0095
Biomass	-0.76	-0.0003	0.00005	0.0000000017
Length	-0.14	0.0000002	0.0000004	0.694
Elevation	-0.04	-0.00005	0.00005	0.328

Global adjusted model $R^2 = 0.613$

Table 6: Results of multiple linear regression analyses of habitat variables on the spring frequency (April-May 2020) of acute heat stress for moose. Upper critical temperature in summer (20°C) and Winter (0°C) as defined by Renecker & Hudson (1986) and daily linear transitions for spring and autumn seasons as defined by Thompson et al. (2020). Moose assumed to have a winter coat from November 1 through May 1, molt from May 1 to July 1, summer coat from July 1 to September 1, and winter coat growth from September 1 to November 1. Data from the Omineca region, North-central BC, Canada.

Coefficient	Zero-order r	Estimate (β)	Standard error	P-value
Closure	-0.26	-0.00003	0.0002	0.874
Biomass	-0.60	-0.0002	0.00004	0.000008
Length	-0.05	0.00000006	0.0000004	0.884
Elevation	-0.02	-0.00003	0.00005	0.542

Global adjusted model R^2 = 0.371