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Behavioural responses of a large, heat-sensitive mammal to climatic variation at multiple spatial scales

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Abstract

1. Climate warming creates energetic challenges for endothermic species by increasing metabolic and hydric costs of thermoregulation. Although endotherms can invoke an array of behavioural and physiological strategies for maintaining homeostasis, the relative effectiveness of those strategies in a climate that is becoming both warmer and drier is not well understood.

2. In accordance with the heat dissipation limit theory which suggests that allocation of energy to growth and reproduction by endotherms is constrained by the ability to dissipate heat, we expected that patterns of habitat use by large, heat-sensitive mammals across multiple scales are critical for behavioural thermoregulation during periods of potential heat stress and that they must invest a large portion of time to maintain heat balance.

3. To test our predictions, we evaluated mechanisms underpinning the effectiveness of bed sites for ameliorating daytime heat loads and potential heat stress across the landscape while accounting for other factors known to affect behaviour. We integrated detailed data on microclimate and animal attributes of moose *Alces alces*, into a biophysical model to quantify costs of thermoregulation at fine and coarse spatial scales.

4. During summer, moose spent an average of 67.8% of daylight hours bedded, and selected bed sites and home ranges that reduced risk of experiencing heat stress. For most of the day, shade could effectively mitigate the risk of experiencing heat stress up to 10°C, but at warmer temperatures (up to 20°C) wet soil was necessary to maintain homeostasis via conductive heat loss. Consistent selection across spatial scales for locations that reduced heat load underscores the importance of the thermal environment as a driver of behaviour in this heat-sensitive mammal.

5. Moose in North America have long been characterized as riparian-obligate species because of their dependence on woody plant species for food. Nevertheless, the importance of dissipating endogenous heat loads conductively through wet soil suggests riparian habitats also are critical thermal refuges for moose. Such refuges may be especially important in the face of a warming climate in which both high environmental temperatures and drier conditions will likely exacerbate limits to heat dissipation, especially for large, heat-sensitive animals.

1 | INTRODUCTION

Earth's climate is warming at an unprecedented pace (Dobrowski et al., 2013; Nunez et al., 2019). Current climate models predict that average global temperatures will increase 1.5°C above pre-industrial levels by mid-century (Masson-Delmotte et al., 2018) and certain regions will experience increased droughts and shifts in precipitation from snow to rain (Berghuijs et al., 2014; Cook et al., 2018). Such rapid warming has resulted in mass mortality events, changes in population abundances, shifts in species ranges, and phenologic shifts in reproductive and migratory events (Pecl et al., 2017; Riddell et al., 2021; Scheffers & Pecl, 2019). Understanding how and to what degree animals can buffer themselves behaviourally and physiologically against energetic costs imposed by a warming climate represents one of the most pressing ecological challenges of our time (Parmesan, 2006; Scheffers & Pecl, 2019).

Warm temperatures can pose a challenge for endothermic animals because of the need to dissipate the considerable endogenous heat produced by normal metabolic processes. Indeed, the Heat Dissipation Limit Theory suggests that allocation of energy to growth and reproduction by endotherms is not constrained by limits to energy intake but instead by the ability to dissipate heat during warmer seasons or other periods of potential heat stress (Speakman & Król, 2010b). Environmental variables such as air temperature, solar radiation, wind and humidity influence the ease with which endotherms can maintain a constant body temperature (Porter et al., 2000, 2002). If the rate of heat input from the environment exceeds the rate of heat dissipation, then body temperature will increase, and the animal will be forced to invoke physiological or behavioural mechanisms to cool, many of which incur energetic and/or water costs (e.g. latent heat loss via cutaneous or respiratory evaporation; Norris & Kunz, 2012).

In addition to external environmental variables, other factors influence heat balance in endotherms. Both morphology and behaviour of endotherms affect how they retain and exchange heat with their environment, and thus their responses to climatic variation (Fuller et al., 2016; Porter & Kearney, 2009). For example, large-bodied endotherms have thicker boundary layers and smaller surface-area-to-volume ratios than their smaller-bodied counterparts, which limits their ability to dissipate heat (Porter et al., 1994). Consequently, as temperatures warm, costs of thermoregulation may increase more for larger species (Fuller et al., 2016; Huey et al., 2012). Although body temperature can be regulated to some degree physiologically (e.g. panting or sweating), behavioural strategies generally are a less costly tool for facilitating heat loss (Fuller et al., 2010; Huey et al., 2012; Long et al., 2014), especially in larger-bodied species. For example, during the hottest, driest part of the year in arid systems, many ungulates such as pronghorn *Antilocapra americana*, oryx *Orxy* spp and African buffalo *Syncerus caffer*, become active during nocturnal hours (Cain III et al., 2006). Therefore, quantifying behavioural responses to the thermal environment and the energetic consequences of those adjustments is a crucial step to understanding how animals will contend with and persist with changing climates (Parmesan, 2006).

Reducing activity (e.g. bedding down) during daytime hours when temperatures are warm is one way endotherms can mitigate the risk of experiencing heat stress (Long et al., 2014; Tull et al., 2001). Inactive animals produce less metabolic heat, and vegetation at and around the bed site can reduce radiative heat gain by providing shade (Mysterud & Østbye, 1999; Porter et al., 2000). In addition, during warm periods, animals often seek refuge sites where they can dissipate heat via conductive transfer to a cool surface (Briscoe et al., 2014; Mysterud, 1996; Verzuh et al., 2021; Williamsen et al., 2019). Koalas, for example, rest against tree trunks that are significantly cooler than their surroundings to dissipate body heat when temperatures are high (Briscoe et al., 2014). Given that variation in environmental temperature can have a variety of impacts on animals such as increasing evaporative water loss and limiting activity times (Terrien et al., 2011), temperature can have profound effects on fitness (Huey et al., 2003; Speakman & Król, 2010a). Furthermore, bedding down during the day is a common behaviour for large mammals during hot and dry periods (Terrien et al., 2011; Tull et al., 2001). Selection of bed sites that can serve as effective thermal refuges, therefore, could be an important behavioural strategy for mitigating the effects of a warming climate, especially for large-bodied endotherms (Mysterud, 1996; Verzuh

et al., 2021; Williamsen et al., 2019). The largest species of Cervidae, the moose *Alces alces*, is also one of the most heat sensitive (Broders et al., 2012; Renecker & Hudson, 1986). Moose are large-bodied with correspondingly low surface-to-volume ratios, have dark pelage and lack the ability to sweat (Renecker & Hudson, 1986). Moose populations have declined in recent decades across much of the southern extent of their range in North America (Monteith et al., 2015), and a warming climate may be one of the major drivers of these declines (Weiskopf et al., 2019). Previous studies have documented that moose reduce daytime activity when temperatures are high (Street et al., 2015) and select bed sites with dense canopy cover and wet substrate (McCann et al., 2016; Verzuh et al., 2021). The association between warm temperatures and bed-site selection suggests that use of bed sites may be an important thermoregulatory behaviour. The overall effectiveness of this strategy (e.g. maintaining body temperature within a thermal neutral zone or minimizing evaporative water loss), however, remains unclear, as does the relative importance of different bed-site characteristics for facilitating heat dissipation.

In accordance with the Heat Dissipation Limit Theory, we expected that patterns of habitat use by moose across multiple scales ranging from the bed site to the home range are critical for behavioural thermoregulation during periods of potential heat stress. Furthermore, we expected that during warm periods, large mammals must invest a substantial portion of time to maintain heat balance (i.e. through reduced activity). Our goal was to quantify the degree to which bed-site selection by moose helps to facilitate heat dissipation and mitigate the risk of heat stress. Furthermore, we sought to evaluate the potential implications of heat stress on habitat selection at the scale of the home range while taking into account other factors that influence habitat selection (e.g. forage characteristics and mortality risk). We used a biophysical model, Niche Mapper, to estimate metabolic costs and the relative risk of experiencing heat stress by moose both within their home ranges and at bed sites under varying scenarios (e.g. an inactive, bedded moose under current climate conditions, a standing, inactive moose under current climate conditions, a moose bedded at a site with shade, or bedded at a site with wet ground). We also evaluated the relative roles of air temperature, relative humidity, wind speed, percent canopy cover and soil moisture in determining the relative value of a bed site as a thermal refuge. We tested the following predictions:

1. Moose select bed sites that confer a lower relative risk of heat stress than randomly available bed sites. Furthermore, air temperature, canopy cover and the presence of wet soil will be key determinants of the risk of heat stress and will enable moose to maintain homeostasis at the bed site.
2. Moose will spend a greater proportion of daylight hours bedded as temperatures increase throughout the summer.
3. Moose will select home ranges that reduce their relative risk of experiencing heat stress, compared with randomly available home ranges.

2 | MATERIALS AND METHODS

2.1 | Study area

We studied adult, female moose *Alces alces shirasi* in the Snowy Mountain Range of the Medicine Bow National Forest in southeastern Wyoming (210,526 ha; Dillon et al., 2005). Elevation ranged from approximately 1915 to 3652 m above sea level, and daily maximum temperature ranged from −46°C during winter to 43°C in summer (Dillon et al., 2005). Daily maximum temperatures in summer typically occurred between 10:00 h and 16:00 h. Snow was the primary form of precipitation at high elevations, with most snowfall occurring between November and April. Total annual precipitation ranged from 38 cm (low elevations) to 100 cm (high elevations; Baigas et al., 2010). Roughly 78% of the study area was forested, the majority of which (~65%) was dominated by lodgepole pine *Pinus contorta*. The study area supported a population of approximately 275 moose (Wyoming Game and Fish, 2018). Moose occupied the full range of elevations in the study area and thus were exposed to the entire spectrum of temperatures and available landcover types. In addition, the area had no resident wolf packs *Canis lupus* or grizzly bears *Ursus arctos*, both of which are known to influence moose distribution and habitat use (Ballard et al., 1991).

We conducted our study during summer (June–September), 2018–2019. Moose transition to summer pelage between late May and early June, and back into winter pelage between late September and early October (Franzmann et al., 2007). Accordingly, we defined summer as the period when moose were in summer pelage (June–September). Calving for moose in this system typically begins in early June but may begin as early as May. The rut and hunting season both start in September (archery only during September, rifle during October). During March 2018, we captured and fit 28 adult female moose with Iridium satellite GPS collars (ATS; Isanti, MN). The collars were programmed to collect hourly locations for each moose. We filtered GPS data so that only fixes that were high quality (i.e. 3D & HDOP <2; D'eon & Delparte, 2005; Moen et al., 1997) were included in our analyses. All animal handling was approved by the Institutional Animal Care and Use Committee at the University of Wyoming (permit 20181218KM00331-01).

2.2 | Niche mapper: Model parameterization

Niche Mapper estimates the metabolic and hydric costs incurred by an animal to maintain homeothermy in a given environment by solving a heat energy and mass balance equation (Kearney et al., 2009; Long et al., 2014, 2016; Porter et al., 2000; Porter & Gates, 1969; Porter & Kearney, 2009; Rogers et al., 2021). Niche Mapper integrates two sub-models, a microclimate submodel and an endotherm submodel, that combine diverse data on the animal species and its environment to predict hourly metabolic rates, and other responses such as water requirements, necessary to maintain homeostasis under user-specified climatic conditions. When

temperatures are warm, Niche Mapper solves the energy balance equation by first allowing the animal to respond behaviourally (e.g. by changing orientation to the sun, seeking shade, retreating to a burrow or seeking water if the user specifies that these options are available). If these behavioural adjustments are insufficient for maintaining internal heat balance, the animal can then respond physiologically by panting or sweating. Because panting and sweating incur both metabolic and hydric costs, the model represents a 'best-case' scenario in which the least costly options for thermoregulation are used first. Finally, if all behavioural and physiological responses are exhausted and the animal remains in a heat-gain situation, the model solves the energy balance equation by reducing metabolism below basal metabolic rate (BMR). This unrealistic result indicates that the animal is at risk of experiencing heat stress. By manipulating the environmental parameters of the microclimate submodel (e.g. incrementally increasing temperature or the amount of shade) or manipulating behaviours of the animal in the endotherm submodel (e.g. allowing the animal to lay on wet ground), the user can effectively parse the main drivers of thermoregulatory costs.

We used Niche Mapper at both coarse (i.e. home range) and fine (i.e. bed sites) spatiotemporal scales to understand how the thermal environment influences metabolic rates and behaviour of moose. We used Niche Mapper to map predicted metabolic rates of moose across the landscape (i.e. predictions were calculated iteratively for each pixel [150m^2] in the landscape) during the average day of each month of the summer, focusing on used and available summer home ranges. We then evaluated microsite selection by modelling hourly metabolic costs incurred by moose in used versus available bed sites (see Appendix A for further description) during the average day (with respect to microclimatic conditions) of each week of the summer. We modelled bed sites as if they were occupied throughout the entire 24-h day so that daytime costs could be directly compared. Moose occupied a variety of bed sites in different habitat types throughout the day and remained bedded in a single site anywhere from 1 to 16h (Verzuh et al., 2021). Moose beds sites were on flat ground; therefore, aspect and slope were not influential factors (Verzuh et al., 2021). By modelling a moose in a single site throughout the day, we were able to determine the thermal qualities of a particular bed site across all daylight hours in which the moose could have been occupying that site. Detailed descriptions of Niche Mapper are provided by Porter et al. (1994, 2000, 2002, 2006) and the accuracy of the model has been widely tested and validated across a wide range of ecosystems and species (Kearney & Porter, 2004; Kearney et al., 2009; Long et al., 2014; Natori & Porter, 2007). We used a metabolic chamber analysis to validate Niche Mapper estimates for moose and conducted a body size sensitivity analysis to determine how sensitive our results were to body mass (Appendix E, Figures E1 and E2). We provide a brief summary below.

We parameterized the microclimate submodel using data obtained from five weather stations for the home-range analysis and from mini weather stations for the bed-site analysis. For a complete description of microclimatic data used in both our home-range and bed-site analyses, see Appendix A. To parameterize the endotherm submodel, we used a combination of data collected directly from live moose (e.g. pelt measurements, body mass and % body fat; Appendix B) and data obtained from the literature (e.g. BMR and average body temperature; Appendix B). We modelled moose in both bedded and standing positions (without increased metabolic rate) for the home-range analysis and in a bedded position for the bed-site analysis.

2.3 | Bed-site selection and the thermal environment

We compared seven competing models to evaluate moose bed site selection. We used generalized linear mixed-effects models (package LME4 in Program R) with a binomial distribution for the error term and a random intercept for animal ID to account for repeated measures to evaluate factors influencing bed site selection of moose and compared models using Akaike information criterion (AIC). We first assessed correlation between predictor variables using Pearson's pairwise correlation coefficients and considered anything >0.4 to be correlated and subsequently removed one of those variables from the model(s). None of our variables were correlated and therefore all were retained in the models. We compared models assessing (1) mortality risk (distance to roads and distance to forest edge), (2) forage (percent willow and integrated Normalized Difference Vegetation Index [iNDVI]) and (3) overheating risk. We then compared all combinations of candidate covariates (e.g. risk and forage, forage and overheating) in a standard model-selection framework. We considered a model to be the top model when ≥2 AIC points lower than the next best model(s).

First, we used Niche Mapper to estimate metabolic rates of moose during the average day of each week of the summer at used and available bed sites to determine if moose selected bed sites that reduced the relative risk of experiencing heat stress. Second, we included distance to roads and distance to forest edge as proxies of risk avoidance. The main natural predators of moose are absent in this system, but hunting by humans does take place. We therefore included distance to roads and distance to forest edge, based on the expectation that if moose are avoiding risk, they should select sites that are farther from roads and closer to the forest edge. To account for variation in the abundance of food resources, we used the percentage of willow in the 15m pixel containing each bed site or random site using a detailed habitat layer (details in Appendix A). Finally, we calculated overall productivity or biomass of vegetation each year of the study as the integrated NDVI (Pettorelli et al., 2005). We calculated iNDVI following the cleaning, smoothing and fitting methods for NDVI data in Bischof et al. (2012) and Merkle et al. (2016). Several ungulate studies have demonstrated the utility of iNDVI as a proxy of vegetation characteristics that can influence herbivore fitness (e.g. abundance and quality of forage), and thus we used this as a metric primarily of forage quality (Hamel et al., 2009; Middleton et al., 2018).

We further evaluated the relative contribution of microclimate parameters, wet ground, canopy cover and landcover type to the thermal environment experienced by moose at bed sites and their respective contribution to the risk of overheating. We averaged weekly conditions in used bed sites in each landcover type (i.e. aspen, pine, wet meadow complex and combined dry) and modelled costs of thermoregulation at those sites during each week of the summer under four different scenarios: (1) high percentage of canopy cover with access to water (i.e. laying on wet soil with 70% of the ventral surface of the animal in contact with the ground); (2) high percentage of canopy cover without access to water; (3) low percentage of canopy cover with access to water and (4) low percentage of canopy cover without access to water. We reported scenarios that were most common (>50%) for each landcover type for both used and available sites (e.g. high shade and wet ground for used aspen sites, high shade and dry ground for available aspen sites, high shade and dry ground for both used and available pine sites).

To understand how different characteristics of a bed site influenced predicted costs of thermoregulation, and thus the potential for those characteristics to mitigate the risk of heat stress, we varied each microclimate variable (i.e. ambient temperature, wind speed, relative humidity and percent shade) independently while holding other values at their median in two separate scenarios: (1) with wet soil and (2) with dry soil, similar to a sensitivity analysis. We used median values of microclimate variables measured at used bed sites over the entire summer period (2018 and 2019) to simulate average conditions experienced by moose at bed sites. We held cloud cover constant at 10% to represent a sunny day in all simulations. This allowed us to evaluate which bed site characteristics (wet ground, shade, etc.) are most important for moose to effectively behaviourally thermoregulate. A complete list of values used in these simulations is provided in Table C1, Appendix C.

2.4 | Home-range selection and the thermal environment

To evaluate how the thermal environment influenced habitat use by moose at the home-range scale, we first created rasters of predicted metabolic rates during each month for moose across the study area under three scenarios: (1) inactive bedded (i.e. lying down) moose under current climate conditions; (2) inactive bedded moose under predicted high-emissions climate warming (i.e. with 2.5°C increase in temperatures, aligned with predictions of the IPCC RCP8.5 model for the middle of the 21st century) and (3) standing, inactive moose under current climate conditions. We chose these scenarios to provide a comparative estimate at the landscape scale for a bedded animal and how that might change as temperatures warm as well as providing a very conservative estimate by modelling an inactive, standing animal. All scenarios were modelled on dry ground to align with the primary soil moisture type in the study system. We then estimated 95% dynamic Brownian bridge home ranges for 26 adult, female moose during summer, 2018 using hourly GPS data obtained

from those individuals. To simulate available home ranges, we randomly cast 156 points (to create 6 available home ranges for each used home range) within the study area bounded by a 1700-m buffer to prevent available home ranges from falling outside the study area and buffered each point by 1596m to produce 8-km^2, circular home ranges, which is the average size of summer home ranges for moose in this system. We repeated the analysis, subsequently increasing our available sample size until our results stabilized. We then retained the lowest number of available points when results stabilized, which was six available ranges for each used range. We then extracted predicted metabolic rates from Niche Mapper from each pixel in each used and available home range. We calculated the proportion of pixels in each used and available home range that had a predicted metabolic rate below BMR (i.e. pixels where predicted metabolic rates indicated a risk of experiencing heat stress). We extracted factors associated with habitat selection that included risk (i.e. average distance from each pixel to roads and forest edge) and forage (i.e. iNDVI and percent willow). The integrated NDVI values ranged from 6.20 to 103.3, so we therefore considered integrated NDVI values below 50 to be low quality and values greater than 50 to be of high quality. We calculated the proportion of each used and available home range that had high iNDVI values and the proportion of pixels in each home range classified as willow. Finally, we used a generalized linear mixed-effects model with a binomial error distribution and animal ID as the random intercept to account for repeated measures (LME4 package program R) to quantify the influence of thermoregulatory costs, risk avoidance and forage on home-range selection by moose. Similar to the bed-site selection analysis, we first assessed correlation among our predictor variables, removing those with correlation values >0.4. Distance to forest was positively correlated with overheating risk (0.56) and thus we removed distance to forest from the models. We compared seven competing models using AIC. We considered any model that was ≥2 AIC points lower than the next best model to be the top model. We also conducted a complementary analysis in which we compared used home ranges with available home ranges comprised of similar habitat, the details of which can be found in the supplementary materials (Appendix D, Table D1).

2.5 | Movement state analysis

We used a two-step approach to evaluate factors that influenced the amount of time moose spent inactive during daylight hours (defined as sunrise to sunset, adjusted daily). First, we used a discrete time and space, two-state hidden Markov model (MOVEHMM package in Program R; Michelot et al., 2016) to estimate the percentage of daylight hours moose spent inactive. Hidden Markov models are state-space models that assume that the distribution of the observations (e.g. GPS locations) is conditional on a finite number of unobservable hidden discrete states (e.g. behaviours) and have been used extensively in ecology on a range of taxa from large mammalian predators to fish and birds (Hamilton et al., 2018;

Pirotta et al., 2018; Baker et al., 2019). Our aim was to classify each hourly GPS location as either active or inactive and to examine two 'hidden' behavioural states, foraging and resting (i.e. active and inactive), we therefore restricted the model to only identify two behavioural states. We calculated step intervals (Euclidian distance between subsequent GPS locations) and turning angles (change in direction between time intervals) that the model then used to determine the most likely behavioural state of the animal based on movement trajectory, speed and distance. The model assigns behavioural states to each individual GPS location for each individual animal and creates a plot of the movement path. We visually inspected the diagnostic plots (Appendix F, Figure F1) of a series of movement trajectories to ensure that the assigned states were reasonable (i.e. locations assigned as resting were clustered and locations assigned to foraging were along a path). The mean step length for the inactive state was 27.72 m with a mean turning angle of 3.05° while for the active state mean step length was 288.86 m and mean turning angle was 0.06.

For the second stage of the analysis, we used generalized linear mixed-effects models (package GLMMADMB in Program R) with a beta distribution for the error term to evaluate factors influencing activity patterns of moose. Our response variable was the proportion of the day spent inactive and our explanatory variables were month (categorical fixed effect; June was our reference), average daily temperature (°C), and an interaction between month and average temperature. To account for autocorrelation of subsamples (i.e. locations) within each sampling unit (moose-years), we included random intercepts for animal ID and year. We considered covariates with a 95% confidence interval that did not overlap zero to be significant predictors of moose activity (Gelman & Hill, 2007).

We collated ambient temperature data from five weather stations that we installed throughout the study system to understand the effect of temperature on moose activity patterns. We mounted HOBO 12-bit temperature sensors in radiation shields and fit them along with a relative humidity sensor on a 2-m tripod with a HOBO wind sensor set (measures wind speed and direction) attached to a cross arm at the top of each station. We used HOBO micro-station data loggers programmed to record weather data every 5 min continuously throughout the day. We installed each station in a different landcover type; aspen, intact pine, beetle-killed pine, sagebrush and riparian. We assigned ambient temperature data from the nearest ($\bar{x} = 11.12$ km, median = 0.88 km) weather station to each moose location for our analysis of temperature effects on moose activity.

3 | RESULTS

3.1 | Bed-site selection and the thermal environment

Moose selected bed sites that conferred a lower overheating risk and that had a higher percentage of willow available in the surrounding 15 m than random bed sites (RSS 0.95, CI 0.94–0.96 and RSS 1.01, CI 1.00–1.02, respectively; Table 1, Figure 1). The top model was the full model that included distance to roads, distance to forest edge, percent willow in the surrounding 15 m, integrated NDVI and predicted overheating risk (△AIC 3.64 between the top and next best model). Bed sites used by moose had a lower relative risk of experiencing heat stress (17.8% of hourly predicted metabolic rates below BMR, indicating heat stress risk) than available bed sites (28.1% of hourly predicted metabolic rates below BMR; Appendix F, Figure F2). Bed sites where moose could lay in water conferred a lower risk of heat stress than sites without access to water, regardless of percent canopy cover or landcover type except for aspen (Figure 2). Across landcover types, pine bed sites had the smallest proportion of hours in which moose were at risk of experiencing heat stress (Figure 1). Ambient temperature at the bed site played a greater role than wind, shade or humidity in determining costs of thermoregulation, with risk of experiencing heat stress predicted to occur at 8°C when soil in the bed site was dry (i.e. no access to water) and all other microclimate variables were held at their median (Figures 2; Appendix F, Figure F3). Although percent shade was effective at mitigating the risk of heat stress when canopy cover was >70% and the ground was wet, it was insufficient when temperatures exceeded 22°C (Figure 2; Figure F3). The most effective mechanism for maintaining heat balance at the bed site was wet ground (Figure 2; Figure F3). In the absence of water and shade, moose could be at risk of experiencing heat stress at temperatures as low as 8°C. If full shade was included in the model, risk of heat stress occurred later in the day when temperatures reached 8°C on dry ground; however, when moose had access to water to lay in at the bed site, risk of experiencing heat stress was minimal until temperatures rose above 18°C (Figure 3).

TABLE 1 Exponentiated model coefficients, standard errors, 95% confidence intervals and p-values from a generalized linear mixed effects regression evaluating bed site selection by female moose in the Snowy Mountains, WY, USA during summer (June–September)

Predictors	Odds ratios	CI (95%)	*p*-value
Intercept	4.85	2.19–10.73	<0.001
% overheating risk	0.95	0.05–0.96	<0.001
Distance to forest	0.01	0.00–1.09	0.054
Distance to roads	1.75	0.97–3.13	0.061
Integrated NDVI	1.00	0.98–1.01	0.739
% willow	1.01	1.00–1.02	0.002
Random effects			
σ^2	3.29		
τ_{id_year}	0.00		
N_{id_year}	30		
Observations	718		
Marginal R^2	0.211		

Abbreviation: NDVI, Normalized Difference Vegetation Index.

3.2 | Movement state analysis

We obtained 90,937 GPS locations from 28 individual moose from June to September, 2018–2019. On average, moose spent 67.8% (range of daily inactivity values = 1.29%–98.7%) of daylight hours inactive during the summer (Table 2). These values varied widely by individual and by day, with some individuals being very active on the same day others were inactive, and individuals sometimes varying their activity levels considerably from day to day (e.g. spent 77% of one day inactive and then spent 33% of the following day inactive). Proportion of the day spent inactive peaked in June, corresponding to parturition, after which moose increased daytime activity
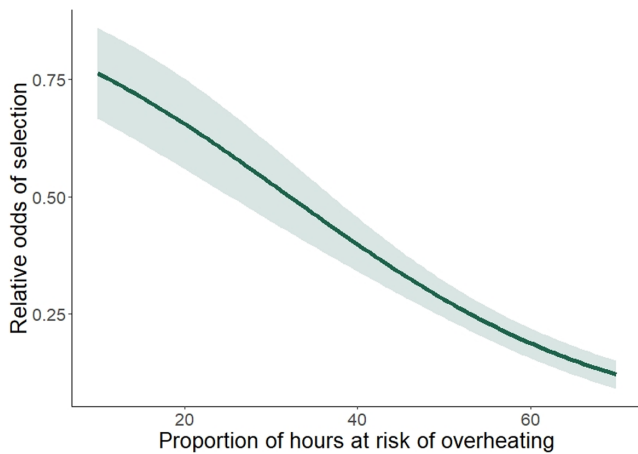
FIGURE 1 Predicted relative odds of selection for a bed site as the proportion of hours at risk of overheating throughout the day increase for female moose in the Snowy Mountains, WY, USA.

(Table 3; Figure 4a,b). While the effect of temperature alone was not statistically significant, the interaction between month and temperature suggested activity was inversely related to temperature during the hottest months of the summer (Table 2; Average temperature × July β = 0.013, 95% CI = 0.001–0.027, August β = 0.013, 95% CI = 0.0004–0.026).

3.3 | Home-range selection and the thermal environment

From June through September, predicted metabolic rates of inactive moose on dry ground indicated relatively high costs of thermoregulation across the landscape based on conditions experienced during the average day of each month. For both a bedded moose under current and warming conditions (i.e. simulated climate change) and an inactive, standing moose, there was a large proportion of the study area with pixels in which moose were predicted to be at risk of experiencing heat stress on the average day of each month (Figure 5). In all three scenarios, July produced the highest proportion of the landscape in which moose were at risk of experiencing heat stress, followed by August (Figure 5). The proportion of the study area in which moose were at risk of experiencing heat stress increased under predicted climate warming (Figure 5). Inactive moose under climate change predictions were able to maintain heat balance in a portion of the study area ranging from 0.3% in July to 23% in September, compared with 3%–36% of the study area (July–September) under current climate conditions, a 2.3% to 13% reduction in thermally suitable habitat.

Moose selected home ranges with less overheating risk, higher percent willow and that were closer to roads than available home

FIGURE 2 Boxplots of predicted metabolic rates of adult female moose at the average used bed site for each landcover type during daylight hours (sunrise to sunset) under the following scenarios in the Snowy Mountain range, WY, USA: (1) maximum canopy cover with access to water (shade, wet ground), (2) maximum canopy cover without access to water (shade, dry ground), (3) minimum canopy cover with access to water (no shade, wet ground) and (4) minimum canopy cover without access to water (no shade, dry ground). The dashed line is the BMR of moose, and values below BMR indicate a risk of experiencing heat stress.
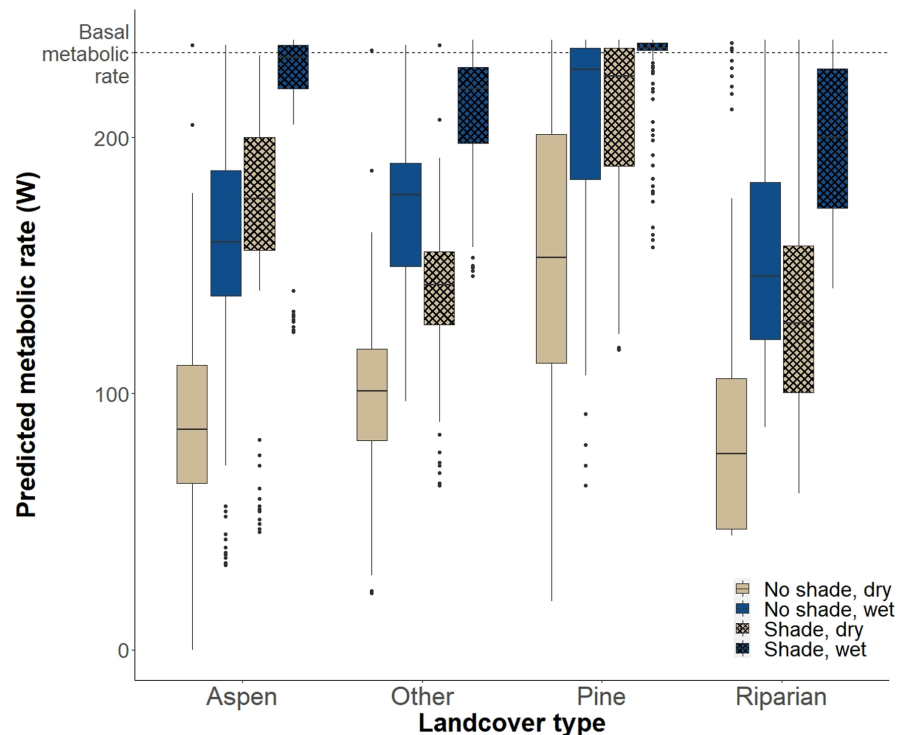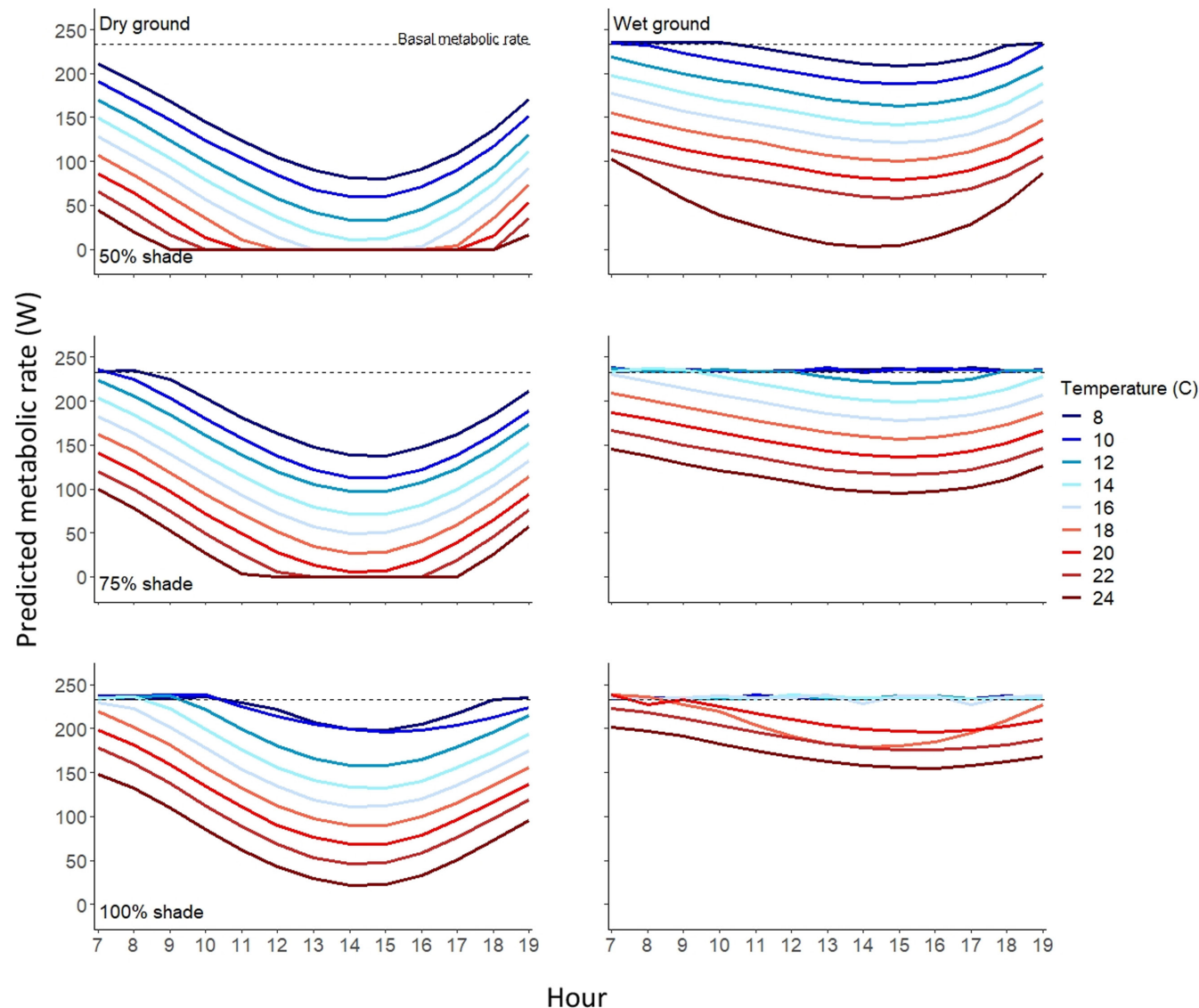
FIGURE 3 Predicted metabolic rates of adult, inactive (i.e. bedded down) female moose during daytime hours in the Snowy Mountain range, WY, USA at an average bed site. Moose were modelled as bedded on either wet (right-hand panels) or dry ground (left-hand panels) with varying levels of canopy cover (0%–100% shade) at air temperatures ranging from 8 to 24°C. dashed black lines represent BMR. When the metabolic rate falls below BMR, the animal is predicted to be at risk of experiencing heat stress.

TABLE 2 Monthly mean and range of ambient temperatures collated from weather stations installed in the Snowy Mountains, WY, USA, during 2018 and 2019. Mean and range of moose activity times (i.e. percent of daylight hours spent inactive by adult female moose) in each month are also presented

| Month | Temperature | | Percent time inactive | |
	Mean ($\bar{x}$) (°C)	Range	Mean ($\bar{x}$)	Range
June	9.09	−7.03–29.19	73.29	1.29–97.74
July	13.00	−3.01–31.36	67.10	10.17–97.76
August	11.68	−4.14–31.94	64.23	9.70–98.03
September	10.35	−9.27–29.94	66.55	8.04–98.17

ranges (Table 4). Furthermore, when selection of home ranges was evaluated via comparison with available home ranges with similar habitat structure, moose strongly selected for less overheating risk,

ranges closer to roads and farther from forest edge (Appendix D, Table D1). Compared with available home ranges, home ranges used by moose had fewer pixels in which moose were at risk of

TABLE 3 Model coefficients, standard errors, 95% confidence intervals and p-values from a linear regression investigating the influence of average temperature and month on the percentage of daylight hours spent inactive by female moose in the Snowy Mountains, WY, USA during summer (June–September). An interaction between temperature and month also was included as a factor. Bolding denotes significant parameters ($p < 0.05$). R^2 for the model was 0.169

Coefficient	Estimate	Standard error	p-value	Upper CI	Lower CI
Intercept	**1.039**	**0.091**	**<0.001**	**0.862**	**1.216**
Temp (°C)	0.004	0.005	0.358	−0.005	0.014
July	**−0.573**	**0.103**	**<0.001**	**−0.776**	**−0.371**
August	**−0.727**	**0.103**	**<0.001**	**−0.929**	**−0.525**
September	**−0.287**	**0.107**	**0.007**	**−0.497**	**−0.077**
Temp × July	**0.013**	**0.006**	**0.034**	**0.001**	**0.026**
Temp × Aug	**0.013**	**0.007**	**0.043**	**0.004**	**0.027**
Temp × Sept	−0.008	0.075	0.283	−0.023	0.007

FIGURE 4 (a) Percent of the day that adult, female moose ($n = 48$) spent inactive (i.e. bedded) during summer (June–September), 2018–2019, in the Snowy Mountains of Wyoming, USA. Daily average temperature (°C) is shown on the primary y-axis while the percent of the day spent bedded is shown on the secondary y-axis. (b) Predicted percent of daylight hours spent inactive (i.e. bedded) by adult female moose during summer months in the Snowy Mountains of Wyoming, USA. Lines with shading represent 95% confidence intervals.
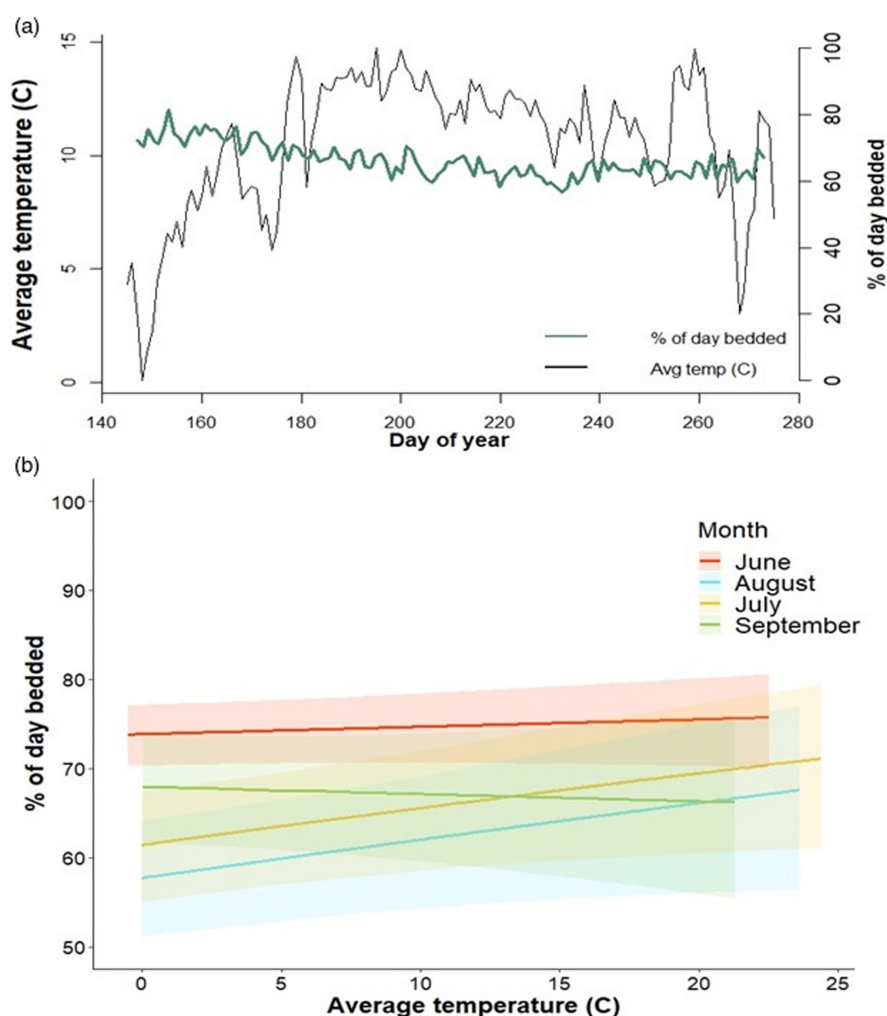
experiencing heat stress during all months of the summer (Figure 6). Differences in area of predicted risk of heat stress were most striking during September, wherein used home ranges had on average 25% less area of predicted heat stress risk than available home ranges ($\bar{x} = 0.382 \pm 0.262$ & $\bar{x} = 0.633 \pm 0.405$ used and available home ranges, respectively).

4 | DISCUSSION

Understanding how changing climatic conditions will affect animal populations requires knowing the degree to which behavioural flexibility allows animals to cope with changing conditions and ameliorate potential population-level effects. Behavioural flexibility,
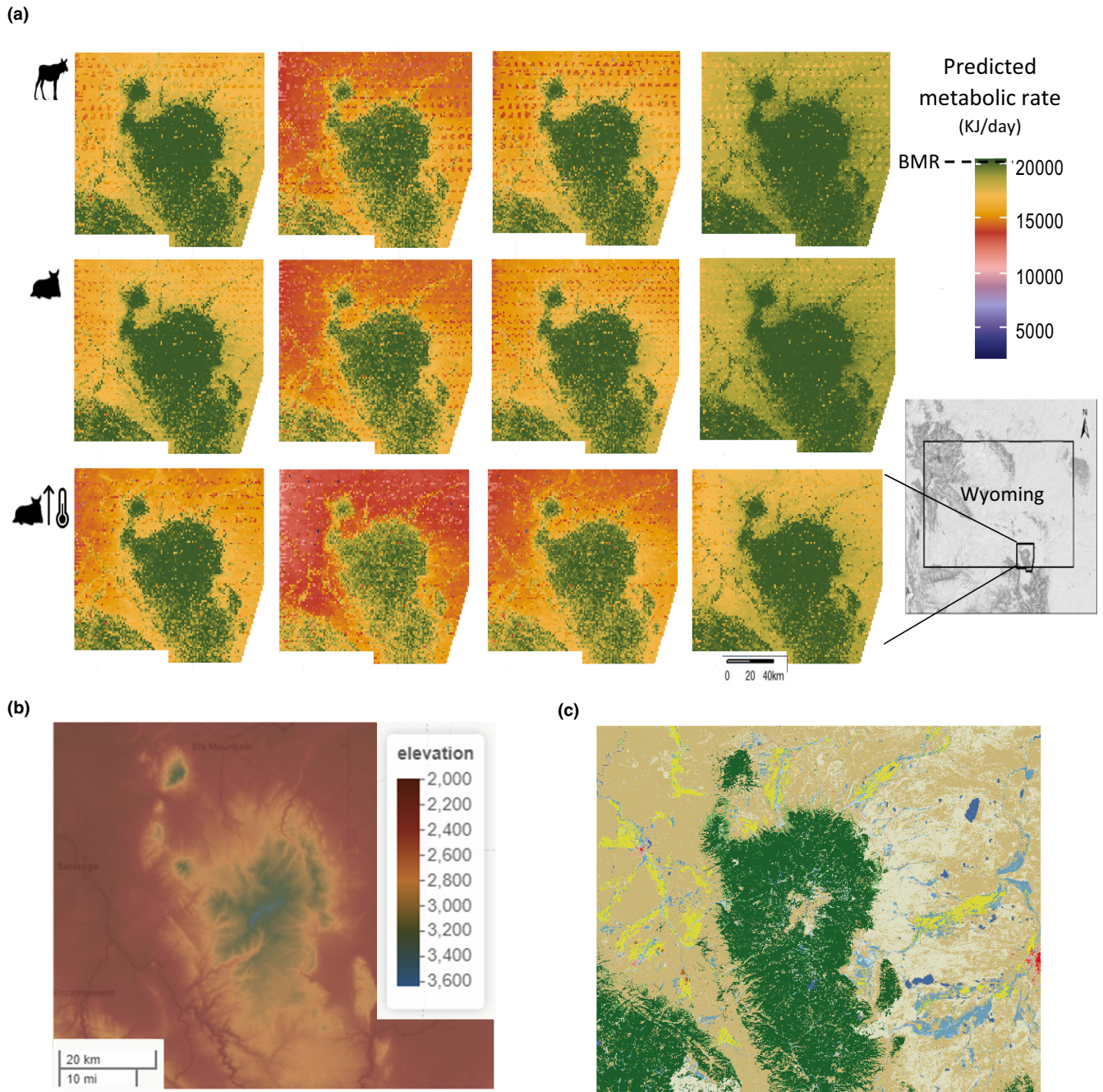
(a)

(b)

(c)

FIGURE 5 (a) Predicted metabolic costs (kJ/day) incurred by moose in the Snowy Mountains of Wyoming, USA, during summer months (June–September). Areas in blue represent metabolic rates close to basal metabolic rate (BMR) and areas in red represent areas of the landscape that pose a risk of heat stress. Top-row panels show predicted risk of heat stress for a standing moose under current climate conditions. Middle-row panels show predicted risk of heat stress for a bedded moose under current climate conditions. Bottom-row panels show predicted risk of heat stress for bedded moose under predicted climate change reflecting the middle of the 21st century (i.e. increased temperatures by 2.5°C). (b) 30 m elevation grid of the Snowy Mountains and surrounding area for reference. (c) Landcover plot of the Snowy Mountains (30 m). Green represents pine, tan and white are bare ground (rock, exposed soil, etc.), blue is water (lakes, rivers, etc.), and yellow represents wet meadows/riparian areas.

specifically the use of day beds that reduce heat gain and selection of home ranges with less overheating risk, was an effective way for moose to mitigate the costs of thermoregulation. This result lends some support to the heat dissipation limit theory and supports our hypotheses that (a) bed sites served as a thermal refuge and (b) that moose would select for habitat that confers a low risk of overheating at multiple spatial scales. Nevertheless, the relative benefits of this strategy were contingent upon specific habitat characteristics, with access to wet ground providing the most effective means of dissipating heat and reducing the risk of experiencing heat stress. Based on our predictive model, the ability of a large mammal to maintain heat balance through a combination of behavioural and physiological

strategies varied greatly depending on a combination of factors (i.e. soil moisture, air temperature, shade; Figures 2 and 3; Figure F3), highlighting the importance of evaluating not just air temperature but also other microclimatic and physical aspects of the environment.

The traits of bed sites chosen by an animal, such as high canopy cover and moist substrate, are often proposed to confer thermoregulatory benefits (e.g. Millspaugh et al., 1998; Verzuh et al., 2021). Selection for cover, however, can be driven by factors other than thermoregulation. Indeed, both red muntjac *Muntiacus muntjak* and sambar *Rusa unicolor* select for bed sites with high levels of cover, although it is not clear whether this is for the benefit of thermoregulation

or the avoidance of risk (Brodie & Brockelman, 2009). Wolves *Canis lupus* select bed sites away from roads and with high levels of cover that are likely to reduce risk of persecution from humans (Llaneza et al., 2016). Site selection may also be influenced by proximity to resources (Mysterud, 1996). For example, red deer *Cervus elaphus xanthopygus* select for bed sites that have high levels of forage and are far from human disturbance (Jiang et al., 2007). Disentangling mechanisms underpinning selection for these traits or other traits that covary with heat stress, however, is difficult without information on the thermoregulatory benefits of the site. In our study, moose selected bed sites that reduced their risk of overheating, and this selection was significant even when taking into account other factors influencing selection (Table 1, Figure 1). The selection of habitat that confers a thermoregulatory benefit at both small and large spatial scales lends additional support to the hypothesis that large, heat sensitive mammals such as moose seek out these spaces to mitigate thermoregulatory costs (Tables 1 and 4).

Many endothermic animals respond to high environmental temperatures by reducing daytime activity (Cain III et al., 2006; Long et al., 2014; Mole et al., 2016). Degus *Octodon degus*, for example, have a bimodal diel activity pattern when temperatures are warm, wherein they reduce activity during the warmest part of the day but maintain higher activity levels and consistent activity patterns in the shade (Bacigalupe et al., 2003), suggesting they may be limited by the amount of heat they can dissipate. Moose spent a large proportion (>60%) of the day inactive during summer months (Figure 4). Heat stress is most likely to occur during summer (Renecker & Hudson, 1986), and moose in other systems respond similarly to warm temperatures by reducing activity (Ditmer et al., 2018; Street et al., 2015). Diurnal reductions in activity of moose in our study were more similar to large ungulates in dry, desert systems than to

TABLE 4 Exponentiated model coefficients, standard errors, 95% confidence intervals and *p*-values from a generalized linear mixed effects regression evaluating home-range selection by female moose in the Snowy Mountains, WY, USA during summer (June–September)

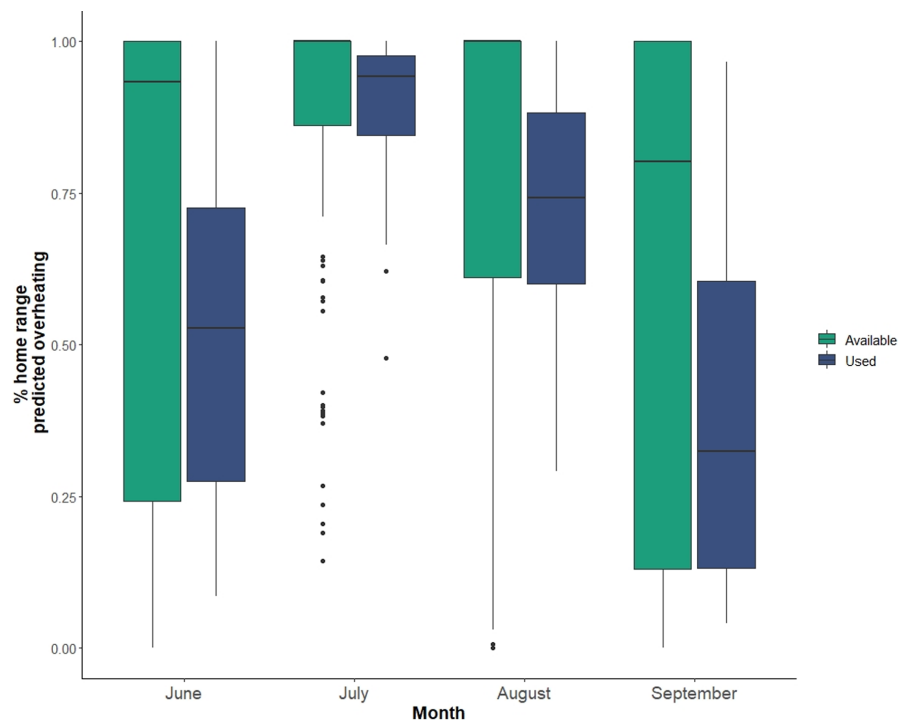| Predictors	Odds ratios	CI (95%)	*p*-value
Intercept	0.82	0.16–4.16	0.807
% overheating risk	0.15	0.03–0.82	0.028
Distance to roads	0.05	0.000–0.90	0.042
% high qual. forage	1.01	0.98–1.04	0.662
% willow	1.47	1.17–1.84	0.001
Random effects			
σ^2	3.29		
$\tau_{id\_year\_season}$	0.00		
$N_{id\_year\_season}$	26		
Observations	153		
Marginal R^2	0.307		

FIGURE 6 Boxplot of the proportion of pixels (150 m^2) in used (*n* = 26, *x* = 8 km^2) versus available (*n* = 156, 8 km^2) moose home ranges in which bedded moose were predicted to be at risk of experiencing heat stress during summer months (June–September) in the Snowy Mountain range of the medicine bow National Forest, WY, USA.

other montane ungulates such as Sardinian mouflon *Ovis gmelinii musimon* that often spend closer to 40% of diurnal hours inactive during warm periods (Jarman, 1977; Merrill, 1991; Pipia et al., 2008). Although reducing daytime activity to mitigate thermal stress is an often-reported behaviour, it may come at the cost of reduced time spent foraging. Animals must continually balance competing needs such as predation risk, foraging and resting, and thermal stress may tip the balance creating additional costs. In our system, however, the most thermally beneficial environments were also those that contained preferred forage and horizontal cover.

Despite being the coolest month of our study period, moose spent the largest proportion of daylight hours bedded during June. Moose give birth in early June, and it is likely that they spent more time bedded immediately before and after parturition compared with other times of the year (McGraw et al., 2014). Parturition also can influence bed site selection. In other large ungulates such as elk *Cervus canadensis*, females select parturition sites with thermal and vegetative cover (Barbknecht et al., 2011). Moose in the eastern United States, however, use a variety of landcover types for parturition sites (McGraw et al., 2014). While moose in this system bedded for longer during June when parturition occurs, the selection of specific bed-site characteristics or the use of specific landcover types did not vary markedly throughout the summer. Furthermore, distance to forest and distance to roads were not significant variables in our bed site model, suggesting that moose are not selecting bed sites solely for risk avoidance. There may be variation in bed site selection depending on reproductive state, but we were unable to test this in our current work because >92% of the females in our study had a calf at heel both years.

In contrast to previous research demonstrating the use of canopy cover by large mammals to mitigate heat stress (e.g. Melin et al., 2014; Mysterud & Østbye, 1999), canopy cover provided only partial relief to moose at their bed sites (Figures 2 and 3; Figure F3). In our study, moose were at risk of experiencing heat stress at temperatures as low as 8°C without canopy cover, whereas under 100% canopy cover, moose at risk of overheating only during the warmest part of the day. When wet ground was available in combination with dense canopy cover, the temperature threshold for the risk of heat stress increased to 18°C (Figure 3). Our wet ground simulations modelled a 50/50 mix of water and substrate, making our results conservative compared with a moose bedded in standing water where heat loss would be more effective. Indeed, moose as well as other large mammals, often seek standing water on hot days (Sawaya et al., 2017; Verzuh et al., 2021). When ambient temperatures were high, use of shade alone was insufficient to maintain heat balance (Figure 3). Indeed, moose were regularly predicted to need to dissipate heat via conduction to wet substrate to avoid heat stress (Figures 2 and 3; Figure F3). Under average summer conditions moose were at less risk of heat stress when they had access to wet soil at their bed sites regardless of canopy cover. Previously documented variation in moose responses to high ambient temperatures (e.g. Ditmer et al., 2018; Melin et al., 2014; Montgomery et al., 2019) may be at least partly explained by varying degrees of canopy cover.

Wet ground and water access play an important role in behavioural thermoregulation by other large mammals such as elephants *Loxodonta africanal* and reindeer *Rangifer tarandus platyrhynchus* (Mole et al., 2016; Williamsen et al., 2019). Moose select for wet substrates at the bed site when temperatures are high (McCann et al., 2016; Verzuh et al., 2021), and our work indicates that doing so may play a central role in their ability to maintain homeostasis in summer. Indeed, for another large mammal (grizzly bears), even small water features are critical to behavioural thermoregulation, specifically for animals that have added constraints from reproductive status such as lactation (Rogers et al., 2021).

In addition to behavioural thermoregulation, large mammals often employ physiological mechanisms such as sweating and panting to reduce heat loads (Porter & Gates, 1969). There are few large mammals that lack the ability to sweat, perhaps because the efficiency of panting for dissipating heat is inversely related to body size (Robertshaw, 2006), thus making sweating more efficient for large species. Indeed, across a range of bovid species of varying body sizes that both sweat and pant, larger animals used sweating more often for evaporative cooling than small animals (Robertshaw & Taylor, 1969). Moose are an exception to this rule and rely on panting for evaporative cooling because they lack the ability to sweat (Dussault et al., 2004). This is in stark contrast to elk, which are a close relative and possess extensive sweating capabilities (Parker & Robbins, 1984). Moose may not have developed the ability to sweat because they rely instead on the abundant wet substrates of their primary habitat for conductive heat loss. Moose have been referred to as riparian obligates, but mostly because of the forage plants that they are uniquely adapted to consume in those locations (Shipley, 2010). We hypothesize that moose may be riparian obligates for needs associated with heat dissipation as well. Future conditions could thereby greatly challenge moose, especially at the southern extent of their distribution, if the very mechanisms (i.e. wet ground) they rely on for behavioural thermoregulation become compromised by climate regimes becoming hotter and drier.

Previous reports of temperature thresholds at which moose begin to alter their behaviour have been varied and inconclusive (Dussault et al., 2004; Lowe et al., 2010; McCann et al., 2013; Melin et al., 2014; Thompson et al., 2020). Results of our study suggest that by selecting bed sites as thermal refuges moose can avoid risk of experiencing heat stress during daylight hours up to temperatures of 24°C if they have access to shade and wet ground, whereas without shade and wet ground they can experience heat stress at temperatures as low as 8°C (Figure 3). This large variation in stress threshold temperatures is consistent with other work showing that moose can experience heat stress at temperatures as low as 14°C (Broders et al., 2012; Renecker & Hudson, 1986), as well as studies indicating that heat stress (or a behavioural response attributed to heat stress) does not occur until temperatures exceed 24°C (Melin et al., 2014; Street et al., 2015). Our predicted heat stress values are lower than previous work likely because we are modelling an animal in a bedded position. Animals that are bedded do have reduced endogenous heat production,

but retain heat compared with a standing animal due to reduced surface area available for heat loss (Figure E1). Furthermore, our results are likely conservative due to modelling moose throughout the entire daylight period instead of limiting our analyses to only the warmest periods of the day.

Moose are one of the most heat-sensitive large herbivores in North America, and considerable research and debate have been devoted to understanding the role of climate warming in the widespread decline of moose populations (Lenarz et al., 2010; Monteith et al., 2015; Renecker & Hudson, 1986). Temperatures experienced by moose at the southern extent of their range frequently exceed proposed thresholds for heat stress (Renecker & Hudson, 1986), suggesting strong potential for climate-mediated effects on fitness. Moose in our study spent a large portion of summer daylight hours inactive (Figure 4), and selected home ranges and bed sites that reduced the risk of experiencing heat stress relative to what was available in the landscape more generally (Figure 6; Figure F2). Our results are consistent with the notion that the thermal environment may restrict moose distribution and selection of home ranges, and support our hypothesis that moose use bed sites as thermal refuges. In addition, as the climate warms, the thermal environment has the potential to restrict moose habitat by as much as 13%. Given that the range of moose may already be limited by summer temperatures (Renecker & Hudson, 1990), access to habitats that provide thermal refuge could be critical for the persistence of southern moose populations.

Climate models predict that the climate will not only become warmer, but in certain regions will also become drier (Berg & Sheffield, 2018; Cook et al., 2018). Our models showed that for moose, simply having wet ground to bed down on could effectively buffer them from heat stress by increments of 10°C or more (Figure 3). Furthermore, precipitation regimes for the western United States are predicted to shift from snow to rain (Berghuijs et al., 2014; Knowles et al., 2006). A shift such as this could reduce not only the persistence, but also the number of ephemeral wetlands that provide thermal refuge (Knowles et al., 2006). Although previous work has focused on the effect of drought on food availability for moose (Monteith et al., 2015), it could be that drought will be far more influential and limiting for moose populations by reducing the ability of moose to behaviourally thermoregulate. Future research that addresses how vegetation and habitats may shift as a result of climate change would provide a clearer picture of how behaviour and habitat selection may be altered due to warming temperatures.

Understanding the effectiveness of behaviour in mitigating temperature changes associated with climate is a pressing need in modern ecology. Our work demonstrated that bed sites may serve as a critical thermal refuge for a large mammal, allowing them to maintain internal body temperatures by dissipating heat through conduction with wet soil. In addition, by identifying the mechanisms that underpin the role of bed sites as thermal refuges and by identifying areas on the landscape with the lowest overall energetic costs, we can more easily predict future changes in animal distributions and determine the relative importance of landscape features in heat dissipation and ultimately, species persistence. Understanding how populations on the fringes of their range respond to changes in the environment can help inform conservation and management efforts through the identification of areas that are of greatest value to animals as they attempt to mitigate the effects of a warming climate.

CONFLICT OF INTEREST

All authors report no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.5tb2rbp7s (Verzuh et al., 2022). All GPS data are available on MoveBank.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1

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