







Thermal constraints on energy balance, behaviour and spatial distribution of grizzly bears

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Abstract

1. Heat dissipation limit theory posits that energy available for growth and reproduction in endotherms is limited by their ability to dissipate heat. In mammals, endogenous heat production increases markedly during gestation and lactation, and thus female mammals may be subject to greater thermal constraints on energy expenditure than males. Such constraints likely have important implications for behaviour and population performance in a warming climate.
2. We used a mechanistic simulation model based on the first principles of heat and mass transfer to study thermal constraints on activity (both timing and intensity) of captive female grizzly bears *Ursus arctos* in current and future climate scenarios. We then quantified the relative importance of regulatory behaviours for maintaining heat balance using GPS telemetry locations of lactating versus non-lactating female bears from Yellowstone National Park, and assessed the degree to which costs of thermoregulation constrained the distribution of sampled bears in space and time.
3. Lactating female bears benefitted considerably more from behavioural cooling mechanisms (e.g. partial submersion in cool water or bedding on cool substrate) than non-lactating females in our simulations; the availability of water for thermoregulation increased the number of hours during which lactating females could be active by up to 60% under current climatic conditions and by up to 43% in the future climate scenario. Moreover, even in the future climate scenario, lactating bears were able to achieve heat balance 24 hr/day by thermoregulating behaviourally when water was available to facilitate cooling.
4. The most important predictor of female grizzly bear distribution in Yellowstone, regardless of reproductive status, was elevation. However, variables associated with the thermal environment were relatively more important for predicting the distribution of lactating than non-lactating female bears.

5. Our results suggest that the costs of heat dissipation, which are modulated by climate, may impose constraints on the behaviour and energetics of large endotherms like grizzly bears, and that access to water for cooling will likely be an increasingly important driver of grizzly bear distribution in Yellowstone as the climate continues to warm.

KEYWORDS

behaviour, genetic programming model, Greater Yellowstone Ecosystem, heat dissipation limit theory, lactation, spatiotemporal distribution, thermoregulation, *Ursus arctos*

1 | INTRODUCTION

Climatic variation directly affects the behaviour and distribution of endothermic animals by determining the costs (i.e. metabolic rate and evaporative water loss) of maintaining homeothermy, and thus the amount of discretionary energy available for growth and reproduction (Porter et al., 2000). Although the magnitude of those costs varies widely among species and habitats, the heat dissipation limit theory (Speakman & Król, 2010a) posits that allocation of energy to growth and reproduction by endotherms is governed more by their capacity to dissipate heat than by their ability to harvest energy from the environment. Even at basal levels, a considerable amount of heat is generated as a by-product of normal metabolic processes, and when environmental temperatures are warm this heat must be dissipated to maintain a stable core temperature. Reproduction (i.e. gestation and lactation) and activity (e.g. traveling or foraging) further increase endogenous heat production, and the amount of energy that can be devoted to growth, reproduction or activity in endotherms may therefore be constrained by their capacity to dissipate that heat, even if energy supplies are effectively unlimited (Król et al., 2003; Król & Speakman, 2003a, 2003b; Speakman & Król, 2010a, 2010b).

Because endogenous heat production increases markedly during gestation and lactation (Bowers et al., 2009; Speakman & McQueenie, 1995; Urison & Buffenstein, 1995), climate warming may constrain energy allocation by female mammals to a greater degree than their male counterparts. Indeed, this difference may have contributed to the evolution of sexual size dimorphism in some species (e.g. European red deer; Post et al., 1999). Limitations on the ability of female mammals to dissipate heat generated by reproduction and activity likely have important implications for female fitness, and thus population performance, in a warming climate. For example, increasing the environmental heat load experienced by female mammals may reduce their ability to devote energy to reproduction, thereby decreasing milk production and subsequent offspring body mass or litter size (Król et al., 2003; Król & Speakman, 2003a, 2003b). Similarly, warming temperatures may limit the timing or duration of daily activity periods (Creel et al., 2016; Hall & Chalfoun, 2018; MacHutchinson et al., 1998).

Grizzly bears *Ursus arctos* are a large-bodied, highly adaptable mammal that historically (before European settlement) occupied a wide range of ecosystems and climatic conditions from northern

Alaska and Canada south to central Mexico (Schwartz et al., 2003). Understanding how current or future temperature regimes may constrain behaviour, energy balance and distribution of grizzly bears is important for conservation and management of this iconic species. Yet, mechanistic relationships between spatiotemporal variation in the thermal environment and behaviour or performance of grizzly bear populations have received little attention. Like most large-bodied mammals, grizzly bears have slow life histories; females typically reproduce for the first time between 4 and 9 years old, with reproductive intervals ranging from 2.6 to 5.6 years and a typical litter size of two cubs (Ferguson & McLoughlin, 2000; Schwartz et al., 2003). Although the inverse relationship between body size and the pace of life is well-known (Dobson & Oli, 2007; Sibly & Brown, 2007), Speakman and Król (2010b) recently suggested that limits to heat dissipation may be the mechanism underlying this phenomenon. If endotherms are constrained by their maximum ability to dissipate heat, then the low surface-area-to-volume ratio of large mammals likely limits their ability to dissipate the additional heat generated by reproduction (Fuller et al., 2016), leading to a slower life history (Speakman & Król, 2010b).

The more limited ability of large mammals to dissipate heat also suggests that in areas with warmer climates, species like grizzly bears may be forced to invest relatively more time (i.e. reduced activity) and resources (i.e. energy and water) into maintaining homeothermy. Although large mammals exhibit a wide array of thermoregulatory strategies, regulatory behaviours (e.g. seeking shade) generally are less costly than physiological thermoregulation, and often serve as the primary buffer against negative effects of environmental variation on fitness (Huey et al., 2003; Long et al., 2014). In a unique example of such behaviours, Gunther et al. (2015) and Sawaya et al. (2016) documented the use of 'bath tubs' (i.e. pools of cool water) by grizzly bears in Yellowstone National Park (YNP) and by American black bears *Ursus americanus* in western Montana, USA during summer months. Both studies suggested that the behaviour served a thermoregulatory function, but that hypothesis has not been tested, and the relative contribution of behavioural thermoregulation to grizzly bear life-history strategy is poorly understood. We sought to fill this knowledge gap and provide general insights into the potential responses of large-bodied mammals to climate warming by (a) collecting detailed physiological, behavioural and environmental data from grizzly bears in both captive and field settings, and

(b) using those data to test hypotheses about effects of the thermal environment on behaviour, energy balance and spatial distribution of grizzly bears in YNP and surrounding areas.

The first objective of our study was to understand the nature and extent of thermal constraints on behaviour (e.g. timing and duration of daily activity) and energy balance of grizzly bears by determining the costs of thermoregulation across a range of temperatures and activity levels using captive bears. Specifically, because grizzly bears are large-bodied endotherms with relatively small surface-area-to-volume ratios, thick boundary layers and thick coats of insulating fur, we hypothesized that: (H1) Grizzly bears invoke behavioural and physiological mechanisms of thermoregulation (e.g. the use of shade or water) to sustain relatively low levels of activity throughout much of the active season, but particularly when environmental temperatures peak during summer; (H2) Because of the additional heat load generated by reproduction, lactating female grizzly bears are subject to greater energetic constraints than non-lactating females under the same environmental conditions; and (H3) Warming temperatures predicted by models of climate change over the next century will increase the costs of thermoregulation and may reduce the hours of the day during which female grizzly bears can remain active.

The second objective of our study was to understand how spatiotemporal variation in costs of thermoregulation affects the distribution of grizzly bears. Previous investigation of the determinants of grizzly bear distribution have focused on the role of food resources and the perception of risk (Nielsen et al., 2010). Similarly, studies of the potential impacts of climate change on grizzly bears have focused mostly on predicted changes in the distribution of food resources (i.e. indirect effects of climate change; Roberts et al., 2014). The potential role of human disturbance in limiting the distribution of grizzly bears also has been evaluated (e.g. Apps et al., 2004; Northrup et al., 2012). To date, however, no studies have evaluated the relative importance of spatiotemporal variation in costs of thermoregulation as a determinant of grizzly bear habitat use and distribution. We evaluated the relative influence of energetic costs imposed by the thermal environment on the distribution of grizzly bears in YNP and surrounding areas, and we tested the following hypotheses: (H4) The landscape-scale distribution of grizzly bears is influenced more by spatiotemporal variation in the thermal environment than by habitat type or human disturbance during the warm summer months; (H5) Because of the additional heat generated by lactation, costs of thermoregulation will have a relatively greater influence on the distribution of lactating than non-lactating female bears.

2 | MATERIALS AND METHODS

2.1 | Energetics modelling: Niche Mapper

We estimated costs of thermoregulation experienced by grizzly bears in a variety of different scenarios and habitats using Niche Mapper (Natori & Porter, 2007; Porter & Mitchell, 2006). Niche

Mapper is a mechanistic model based on biophysical first principles that estimates the metabolic and hydric costs of maintaining homeothermy under a specified set of environmental conditions by solving the energy balance equation for the modelled species (Mathewson & Porter, 2013; Porter & Gates, 1969; Porter et al., 1994, 2010). Niche Mapper consists of two submodels: a microclimate model and an endotherm model. These two submodels integrate a suite of data on the animal and its environment to predict hourly rates of water loss and metabolism necessary to maintain core temperature within a user-specified range at a specific location and time (Huang et al., 2013; Long et al., 2014; Natori & Porter, 2007).

The microclimate submodel uses climate data supplied by the user to calculate hourly profiles of air temperature, wind speed, humidity and solar radiation 2-m above the ground during the 'average' day within a user-specified time interval (often a week or a month, although any time interval can be used). The model assumes that each average day is representative of all days within the specified temporal window; therefore, the length of the time interval is typically chosen to ensure that this assumption is reasonable without requiring undue processing time. The accuracy of Niche Mapper's microclimate model has been widely tested and validated across a range of ecosystems (e.g. Huang et al., 2013; Kearney et al., 2014; Mitchell et al., 1975; Natori & Porter, 2007; Porter et al., 1973).

We parameterized the microclimate model for our evaluation of thermoregulatory costs using data from a HOBOware weather station and data logger placed along the perimeter of the captive grizzly bear enclosure at the Washington State University Bear Research, Education, and Conservation Center (hereafter BRECC) during summer (May through September), 2018. The weather station recorded air temperature, wind speed and relative humidity at 5-min intervals at 2-m above the ground. We obtained data on daily cloud cover from a public database hosted by WeatherUnderground (<https://www.wunderground.com/>). We calculated weekly averages of the daily minimum and maximum values for each climate variable (i.e. values were averaged across all 7 days within each week), and then fed those averages into the microclimate model. In addition, to estimate the costs of thermoregulation in a warming climate, we reparameterized the microclimate submodel with temperature data that aligned with predictions of the IPCC AR5 RCP 8.5 model for the middle of the 21st century in our study region (i.e. we added 2.5°C to our empirical measurements of average high and low temperatures; all other microclimatic variables were held at their empirically measured values). Scenario RCP 8.5 is a 'business as usual' scenario that assumes no mitigation of emissions and atmospheric concentrations of greenhouse gases (IPCC, 2014).

The endotherm submodel integrates various properties of the animal that influence rates of heat and mass transfer (e.g. fur depth, pelt reflectivity, metabolic rate; Long et al., 2014; Mathewson et al., 2017; Natori & Porter, 2007) in concert with vegetation characteristics and the output from the microclimate submodel. Together, output from the endotherm and microclimate submodels define the animal's thermal environment (Appendix A). To solve the energy balance equation for the animal at each time step, the animal is allowed to

thermoregulate both behaviourally and physiologically. To model a 'best-case scenario', we allowed the animal to perform a series of behavioural responses (i.e. seeking shade) first before resorting to physiological responses (i.e. panting or sweating) that invoke a metabolic or water cost. When energy and water must be expended to maintain heat balance, these costs are reported as hourly estimates by the model. Multipliers of basal metabolic rate (BMR) can also be used to account for different levels of physical or reproductive activity (e.g. lactation). If the model animal remains in a 'heat-gain' situation after exhausting all mechanisms of behavioural and physiological thermoregulation, Niche Mapper solves the energy balance equation by forcing the metabolic rate of the animal to drop below the target rate. This unrealistic result indicates significant risk of heat stress characterized by increased core body temperature, excessive panting, and, if left unchecked, the potential for mortality to occur.

To parameterize the endotherm model for grizzly bears, we obtained pelt and body measurements from five adult female bears at the BRECC, two of which were obtained from YNP as adults and three of which were produced at the BRECC by females from northwest Montana and fathered by males from north-central British Columbia (Robbins et al., 2018). We measured hair length and fur depth with a digital caliper. Fur density (hairs/cm²) was calculated from samples shaved from each bear. We measured the area of the shaved patch using a digital caliper and counted the number of hairs in five subsamples from the total shaved sample. We then weighed each subsample to establish the relationship between subsample mass and number of hairs and estimated the total number of hairs in the full-shaved sample as a function of its mass. Finally, we estimated fur density by dividing the estimated number of hairs in the shaved sample by the area of the shaved patch. Grizzly bears have two fur types, guard hairs and underfur. We used underfur measurements for parameterizing the endotherm model, because our analyses revealed that the coat was comprised of 96.8% underfur hairs by count, and thus the role of the pelt in heat transfer likely was dominated by the underfur. The width of each hair was determined by photographing individual hairs under a microscope at 100× magnification and then measuring the width using ImageJ software (available from the National Institute of Health Research Services Branch; <https://imagej.nih.gov/>). The endotherm submodel allows pelt characteristics (hair length, diameter, density and pelt depth), body mass and percent body fat to vary through time, so we measured fur properties of captive bears once in May (winter coat) and again in September (summer coat), and then allowed those traits to transition smoothly (i.e. in consistent weekly increments) from winter to summer values during the study period. Body mass and percent body fat also were allowed to change temporally according to monthly measurements of seasonal mass gain from adult female bears in the Yellowstone ecosystem from Schwartz et al. (2014). We measured pelt reflectivity across a range of wavelengths (350–2,500 nm) using an ASD portable spectrophotometer and integrated the resulting curve to estimate total pelt reflectivity. All measured parameters were averaged across individuals, and additional parameters were obtained from the literature (Appendix A). Estimated metabolic rates from Niche Mapper were validated in a metabolic chamber simulation described

in Appendix B. All animal handling was approved by the Institutional Animal Care and Use Committee at the University of Idaho (protocol #IACUC-2018-21).

We quantified energetic costs of activity (i.e. locomotion) using the same five captive adult grizzly bears housed at the BRECC. We measured rates of oxygen consumption by each bear while it walked on a treadmill within a metabolic chamber at differing speeds and inclines (range of speeds = 1.6–4.3 km/hr; range of inclines = –20%–20%). We then used the resulting data to determine an appropriate range of activity multipliers (i.e. increases in energy expenditure above BMR) to use when parameterizing Niche Mapper (Appendix A). Under normal conditions, a bear traveling from a resting place to a known food source travels at ~3.6 km/hr (Craighead, 1976; Shine et al., 2015). Therefore, we used the proportional increase in energy expenditure above BMR experienced by a bear walking at that speed (56%) as the multiplier for modelling an active bear (inactive bear = BMR, active bear = 1.56 × BMR).

To investigate the relative importance of 'bath tubs' (i.e. access to water bodies) as a strategy for thermoregulation by bears (Gunther et al., 2015; Sawaya et al., 2016), we conducted several simulations in which bears were given the option to submerge up to 100% of their torso and 80% of their neck in cool (~14°C) water to achieve heat balance. Similarly, to investigate the benefit of bedding behaviour, we gave simulated bears the option to lay down (body and legs contacting the ground with legs extended) in 1 cm of cool water, and assumed this was equivalent to the cooling effect of the body contacting a cool substrate while bedded. Niche Mapper assumes that if a bear is in a lying posture while bedded, it cannot be active, and so the activity multiplier was not included in the calculation for bedded bears. However, when Niche Mapper models a bear submerged in water, the model bear is assumed to be in a standing posture and Niche Mapper includes the activity multiplier in its calculations. This is consistent with bear behaviour; bears often remain active even while submerging in water (Gunther et al., 2015; Sawaya et al., 2016). We also examined the impact of lactation on heat balance of female bears by using a multiplier (1.52 × BMR; Gittleman, 1989) to account for the additional energetic cost (and associated heat generation) of milk production at peak lactation.

We used Niche Mapper to compare the costs of thermoregulation experienced by captive bears during summer (May–September) in the following scenarios: (a) lactating females at rest versus active and with or without access to water/beds; (b) non-lactating females at rest versus active and with or without access to water/beds; and (c) the same scenarios described in (a) and (b) with a 2.5°C increase in temperature minima and maxima to simulate the effects of climate warming.

Costs of thermoregulation predicted by Niche Mapper can be sensitive to measurement error or other sources of variation in data used to parameterize the model. Therefore we expanded upon the methods of Wang et al. (2018) to evaluate the sensitivity of our results to variation in BMR, costs of activity, costs of lactation, fur depth, hair length, core body temperature, body mass and the temperature difference between inspired and expired air. A detailed description of those analyses and all associated results is provided in Appendices C and D.

2.2 | Analyses of grizzly bear distribution

We used GPS location data from 14 resident (i.e. $\geq 95\%$ of locations occurred within YNP; $n_{\text{lactating}} = 2$, $n_{\text{non-lactating}} = 12$) female grizzly bears during summers (May through September) of 2007 and 2008 to train and validate the models of female grizzly bear distribution in YNP (44.428°N, 110.5885°W; Figure E1, Appendix E) and its surrounding environs. The study area surrounding YNP included other National Park Service, National Forest and private lands. The grizzly bear population was estimated to be near its carrying capacity in core areas of the ecosystem, such as YNP (van Manen et al., 2016; Schwartz et al., 2006). More than 3 million people visited YNP in 2007, resulting in $>40,000$ user nights at backcountry sites, the majority of which occurred between May and September when bears were active (Gunther, 2008). Maximum temperature recorded in West Yellowstone, MT (elevation 2,032 m) in summer (May through August) was 28.9°C in 2007 and 27.2°C in 2008. Elevations in the park range from 1,610 to 3,462 m. Capture and handling of grizzly bears was conducted using methods developed by Blanchard (1983) and Schwartz et al. (2006) and conformed to the Animal Welfare Act and to USA Government principles for the use and care of vertebrate animals used in testing, research and training (USA Geological Survey Animal Care and Use Committee protocol #201201 and University of Idaho protocol #IACUC-2018-21). Additional details can be found in Peck et al. (2017).

We used a landscape-scale application of Niche Mapper to quantify spatiotemporal variation in costs of thermoregulation that could be experienced by grizzly bears within the study area. In the landscape-scale analyses, the microclimate submodel performs simulations using environmental data supplied by the user for each location (i.e. pixel in a raster) and time, and assumes the animal occupies the centre of the pixel. We used an 800 m \times 800 m pixel size to match the spatial resolution of our climate data (see below). The endotherm submodel is then run for each pixel using the hourly microclimate output from the microclimate submodel and the animal data supplied by the user. Spatiotemporally explicit model predictions are assembled into a raster-based map of the energy cost landscape (Long et al., 2014, 2016; Zhang et al., 2018).

To parameterize the microclimate model for the landscape-scale analysis, we used publicly available climate data. We obtained air temperature (monthly averages of daily minima and maxima) and elevation data (800-m resolution) from the PRISM Climate Group at Oregon State University (<http://www.prism.oregonstate.edu/normals/>), which reports 30-year norms for 1981–2010 (Daly et al., 2008). Cloud cover data (percentages) were obtained from EarthEnv datasets (<https://www.earthenv.org/cloud>), which use twice-daily MODIS satellite images integrated over 15 years (2000–2014) to generate monthly average cloud cover estimates (Wilson & Jetz, 2016). We estimated relative humidity using a model subroutine that calculated daily relative humidity as a function of daily temperature range and a constant mass of water in the air. We obtained canopy cover data from the National Land Cover Database 2011 USFS Tree Canopy cartographic data ([\[usfs-percent-tree-canopy-cartographic-version\]\(https://catalog.data.gov/dataset/nlcd2011-usfs-percent-tree-canopy-cartographic-version\); Wickham et al., 2014\). We used percent canopy cover as a proxy for percent shade in each pixel \(Long et al., 2014\), with location-specific estimates of error used to specify the minimum and maximum potential values at each pixel.](https://catalog.data.gov/dataset/nlcd2011-</p>
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We used Niche Mapper to predict the metabolic rates of lactating and non-lactating female grizzly bears with and without access to water for cooling on a monthly basis throughout the study area during May–September. However, in our analysis of grizzly bear distribution (see below), we assumed that bears did not have access to water or bedding for cooling because our goal was to establish a baseline for comparing relative differences in energetic costs experienced by bears moving throughout the study area without behavioural thermoregulation.

To evaluate the relative importance of thermoregulatory costs as a driver of grizzly bear distribution, we obtained data on several additional covariates with demonstrated potential to influence grizzly bear behaviour and distribution. We quantified human occupancy using the 2010 USA Census Bureau Home Density layer (<https://www.census.gov/data.html>). We also calculated the distance of each pixel in the landscape to a major road or highway. We obtained a map of land cover types from the 2011 National Land Cover Data for Conterminous United States database (<https://catalog.data.gov/dataset/nlcd-2011-database>), which separates land cover into 20 distinct categories according to vegetation type and patterns of land use. Data on distance to perennial streams and rivers were obtained at a scale of 1:24,000 from the National Hydrologic Dataset from the USDA Natural Resources Conservation Service Geospatial Data Gateway (<https://gdg.sc.egov.usda.gov>).

We evaluated the influence of a suite of environmental covariates on the distribution of lactating and non-lactating female

TABLE 1 Relative importance of variables from the genetic programming analysis, calculated as the percentage of model runs ($n = 48$) in which the algorithm selected the variable as a predictor in a final best individual (i.e. descriptive statement tree; Appendices F and G) that was more than 70% accurate

Variable	Relative importance	
	Lactating (%)	Non-lactating (%)
Elevation	100.0	100.0
Distance to road or highway	70.8	4.2
Cloud cover	58.3	12.5
Minimum daily temperature	54.2	16.7
Distance to stream or river	45.8	8.3
Census home density	42.7	12.5
Maximum daily temperature	41.7	4.2
Metabolic rate (kJ/day)	33.0	4.2
Percent shade	33.3	12.5
Distance to forest edge	33.3	4.3
Land cover type	25.0	4.2

grizzly bears during summer using an algorithmic genetic programming model (Koza, 1996). Algorithmic models are powerful tools for predicting complex ecological phenomena and have a number of advantages over more traditional statistical approaches (e.g. the ability to deal efficiently with colinear variables; Bhattacharya, 2015; Park & Chon, 2007; Recknagel, 2001). The genetic programming model is a form of evolutionary computation in which solutions to a problem are evolved by improving upon a poorly fitting, randomly generated initial model. Because model convergence can occur at local maxima, evaluating the relative importance of candidate predictor variables requires assimilating the results of a large number of program iterations (i.e. model runs)

into an aggregate frequency table (e.g. Table 1). Variable importance is then inferred from the proportion of model runs in which a variable was included in the 'best' model. A detailed description of the model and our approach to quantifying the relative importance of each covariate is provided in Appendix F. In Figure 1, we illustrate the key conceptual relationships among (a) each of our three core analyses (single-site Niche Mapper simulations, landscape-scale Niche Mapper simulations and the genetic programming model); (b) the datasets used to parameterize the respective models in each analysis; (c) the specific hypotheses each analysis was designed to test; and (d) the specific set of results used to test those hypotheses and where those results are located.

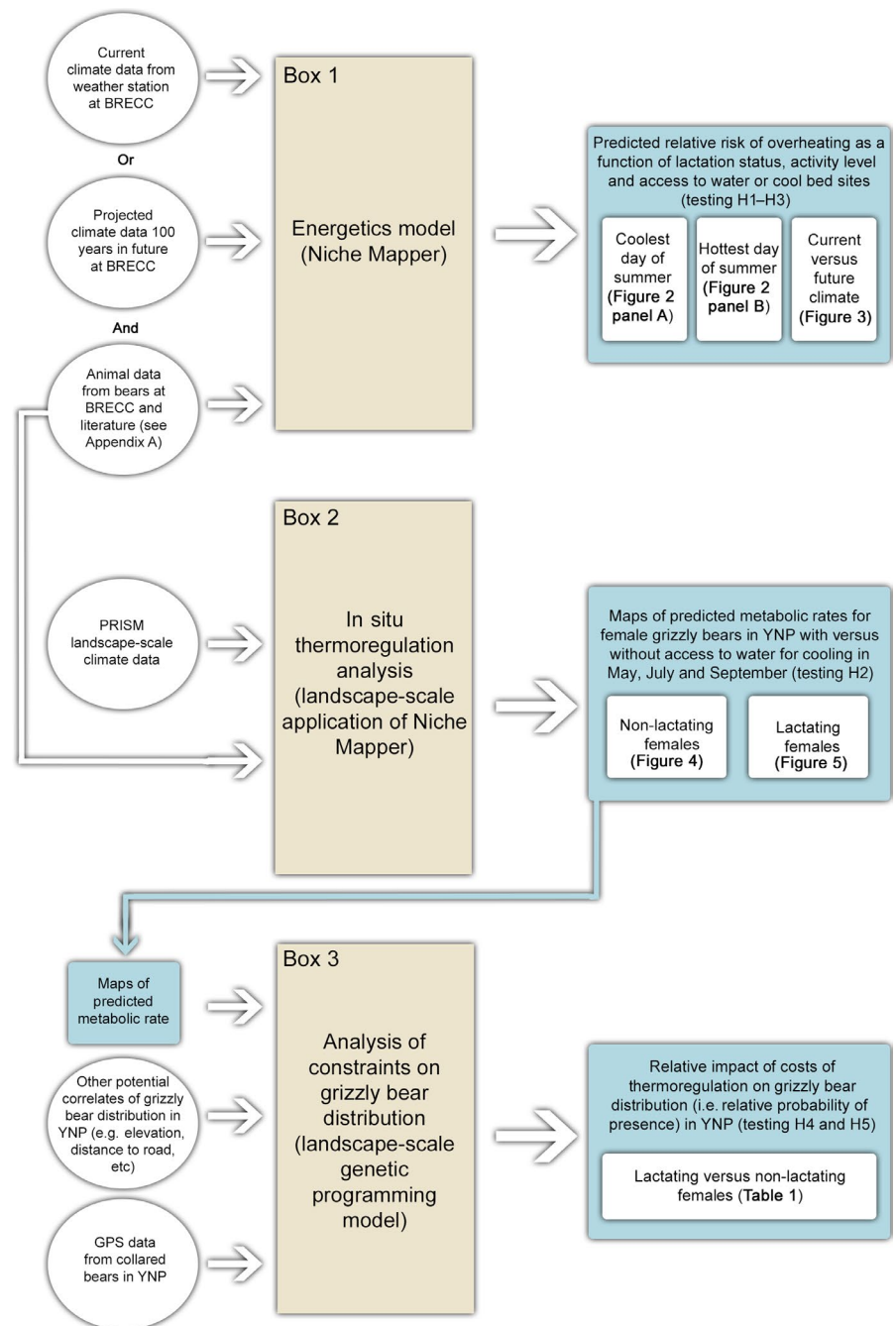


FIGURE 1 Conceptual diagram illustrating key connections among each of the three core analyses in our study: single-site Niche Mapper simulations of grizzly bears at the Washington State University Bear Research, Education, and Conservation Center (BRECC) in Pullman, Washington, USA (box #1), landscape-scale Niche Mapper simulations (box #2), and the genetic programming model of grizzly bear distribution in Yellowstone National Park (YNP; box #3). Also illustrated are the primary datasets used to parameterize the respective models in each step (circles on the left), and how each core analysis relates to (a) the specific hypotheses the analysis was designed to test, (b) the specific set of results used to test those hypotheses and (c) which figures contain those results (boxes on the right)

3 | RESULTS

3.1 | Captive grizzly energetics at the BRECC

During the coolest week of summer, predicted metabolic rates of inactive female bears at the BRECC largely were unaffected by diel variation in environmental temperature regardless of reproductive status (i.e. bears were able to maintain heat balance throughout the day by adjusting conductance, seeking shade, panting or a combination of these; Figure 2). Indeed, during the night bears sometimes had to increase metabolic heat production to stay warm (Figure 2),

and this increase in energy expenditure began up to 5 hr earlier at the lowest calculated values of BMR (Figure C2, Appendix C). This general pattern held for non-lactating, inactive females until July 2, at which point bears that were not allowed access to water for cooling began to experience risk of heat stress during some portion of the day (up to 37.5% of the hottest day of summer, August 6; Figure 3). Lactating female bears without access to water were predicted to be at risk of heat stress as early as June 18 and as late as September 24. On the hottest day of summer, lactating females were at risk of heat stress for up to 45.8% of the day when water was not available for thermoregulation (Figure 3), and bears began

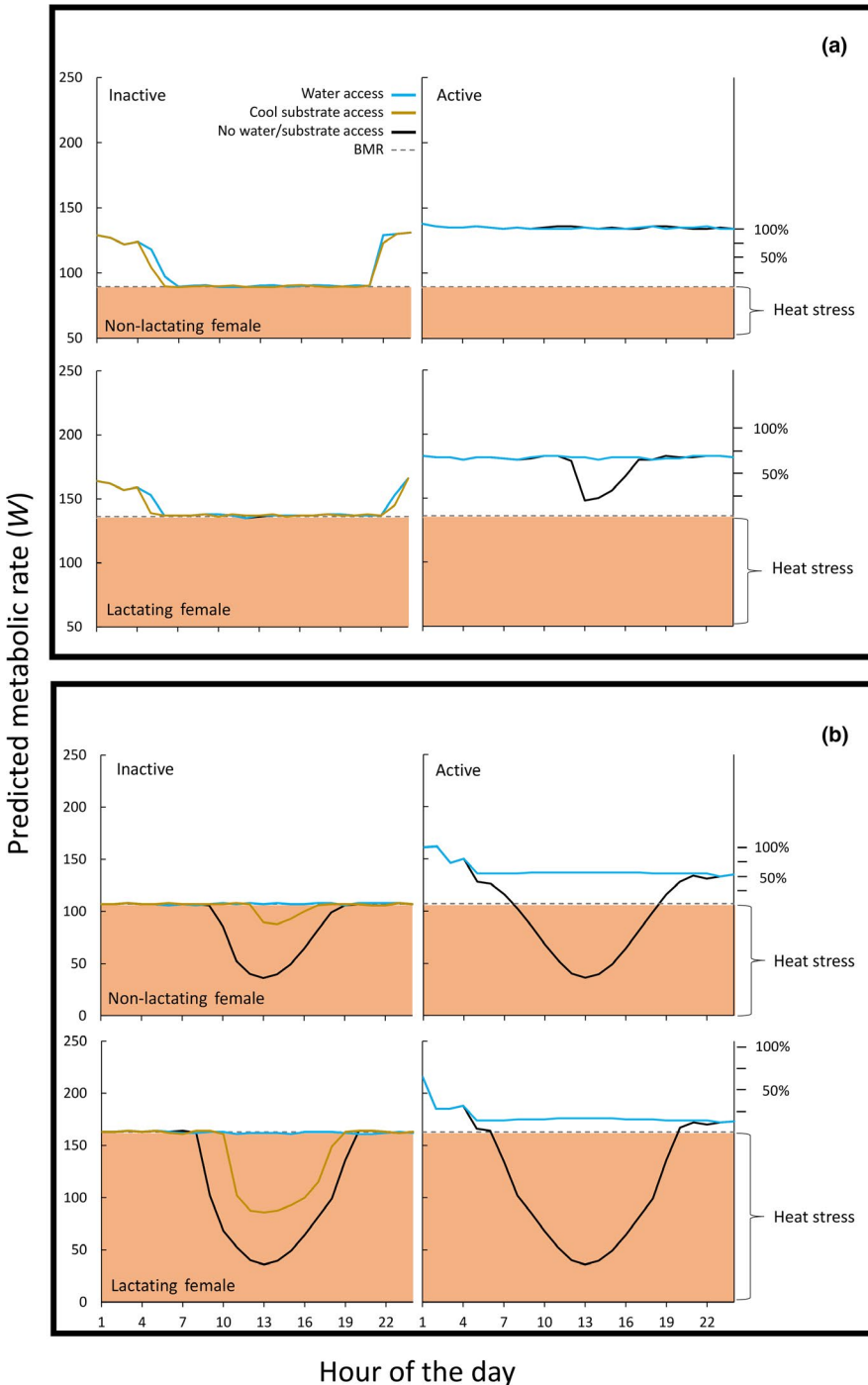


FIGURE 2 Predicted hourly metabolic rates (W) from Niche Mapper for lactating and non-lactating female grizzly bears at low (i.e. inactive: basal metabolic rate, BMR) and high ($1.56 \times \text{BMR}$) activity levels during (a) an average day of the coolest summer week (11–17 June; 102.5-kg bear with 15% body fat) and (b) an average day of the hottest summer week (6–12 August; 130-kg bear with 26% body fat) recorded in 2018 at the Washington State University Bear Research, Education, and Conservation Center in Pullman, Washington, USA. Blue lines represent predicted metabolic rates when bears were allowed access to pools of $\sim 14^{\circ}\text{C}$ water for cooling, tan lines represent predicted rates when bears were bedded on cool substrate (bears bedded on cool substrate cannot be active, so predictions for this condition were excluded from the high activity panels), and black lines represent predicted rates when bears were not allowed to bed or access water for cooling. Basal metabolic rate is denoted by a dashed grey line. The orange-shaded portion of the graph below BMR denotes conditions in which the bear is expected to experience heat stress, such as increased core temperature or excessive panting (predicted metabolic rates below BMR indicate that heat balance is not achievable via the suite of physiological and behavioural mechanisms available). The second Y-axis denotes the percentage of the target metabolic rate for sustaining high activity levels ($1.56 \times \text{BMR}$) that is attainable in the modelled scenario

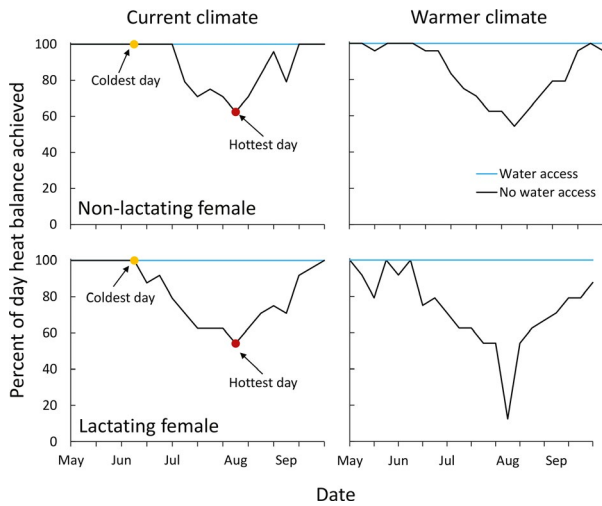


FIGURE 3 Predicted percentage of the day between 7 May and 3 October 2018 during which inactive, non-lactating (top row) and lactating (bottom row) female grizzly bears at the Washington State University Bear Research, Education, and Conservation Center in Pullman, Washington, USA were able to achieve heat balance (i.e. avoid significant risk of heat stress) in both current climate conditions and under a 2.5°C temperature increase. Blue lines represent model predictions when bears were allowed access to pools of ~14°C water for cooling, and black lines represent predictions when bears were not allowed access to water

to experience heat stress up to 4 hr earlier at the highest calculated values of BMR (Figure C3, Appendix C). In contrast, when water was available for thermoregulation, both non-lactating and lactating female bears were able to achieve heat balance throughout the day for the entire summer (Figure 3). Behavioural observation of captive bears corroborated these predictions; during mid- and late-summer, bears consistently either retired to their air-conditioned paddock or submerged in cool water during the middle of the day.

During the coolest and the hottest weeks of summer, the ability to sustain high levels of activity (and associated levels of metabolic heat production) differed between reproductive classes and was influenced by access to water. When temperatures were cool, non-lactating females were able to successfully dissipate the heat produced by a high level of activity (i.e. traveling at 3.6 km/hr; $1.56 \times \text{BMR}$) throughout the day (Figure 2). When temperatures were hot, however, access to cool water played an important role in facilitating activity. Without water, active, non-lactating females were predicted to experience heat stress during the middle of the day (09:00 to 18:00), but were able to sustain up to 56.1% of the target activity level during those hours when water was available for cooling ($1.28 \times \text{BMR}$; Figure 2).

Lactating female bears were unable to sustain a high level of activity at any time of day during either the coolest or hottest weeks of summer. Maximum sustainable levels of activity for lactating females were 67.6% ($1.34 \times \text{BMR}$; Figure 2) and 16.2% ($1.08 \times \text{BMR}$; Figure 2) of the target rate during the coolest and hottest weeks respectively. This result suggests that the additional heat produced by traveling at 3.6 km/hr cannot be fully dissipated by lactating female bears regardless of access to water. Water access did, however,

facilitate a higher level of activity, and effectively buffered lactating females against heat stress even on the hottest day of summer (Figure 2).

Sensitivity analyses indicated that increasing costs of lactation (and thus increasing levels of endogenous heat production) significantly increased the amount of time that female grizzly bears were at risk of heat stress (Appendix C). However, that effect was strongly modulated by environmental temperature and activity level. For example, on the coolest day of summer, non-lactating female bears were at no risk of heat stress during any hour of the day up to an activity level of $1.5 \times \text{BMR}$, whereas females at peak lactation were at risk of heat stress at that level of activity even during night-time hours (Figure C4, Appendix C). Our sensitivity analyses also indicated that costs of thermoregulation predicted by Niche Mapper were more sensitive to variation in core body temperature and body mass than to variation in fur traits or the temperature gradient between inspired and expired air (Appendix D).

For both reproductive classes, temperature increases predicted under climate change scenario RCP 8.5 reduced the number of hours during which inactive bears could achieve heat balance without water access by up to 87.5% (range = 0%–87.5%; Figure 3). Indeed, the proportion of the day during which inactive, non-lactating females were able to achieve heat balance was <100% for most of the summer and declined to as low as 54% in July and August (Figure 3). Lactating females were subject to even greater constraints in a warmer climate and were only able to achieve heat balance during 12.5% of the hottest day of the summer (Figure 3). When water was available to facilitate cooling, however, both non-lactating and lactating females were able to achieve heat balance 24 hr/day throughout the summer by thermoregulating behaviourally (Figure 3).

3.2 | Landscape-scale analyses and distribution modelling

Predicted differences in costs of thermoregulation experienced by lactating versus non-lactating female grizzly bears also were apparent at the landscape scale (Figures 4 and 5). We used the difference between predicted metabolic rates from Niche Mapper and BMR as a measure of the relative risk of a bear experiencing heat stress (predicted metabolic rates below BMR indicate that heat balance is not achievable via the suite of physiological and behavioural mechanisms available). The relative risk of heat stress increased during the hottest parts of the summer (e.g. July; Figures 4 and 5). Importantly, however, when bears were allowed to access water to cool behaviourally (i.e. to submerge in), relative risk of overheating was greatly reduced. Moreover, bears tended to be inactive during hours when relative risk of heat stress was high, but this result was much less pronounced when bears were allowed to use water for cooling (Figures 4 and 5). The proportion of the landscape in which bears were predicted to be at risk of overheating was consistently higher for lactating than for non-lactating females, and this difference was most pronounced in the hottest part of the summer (Figures 4 and 5).

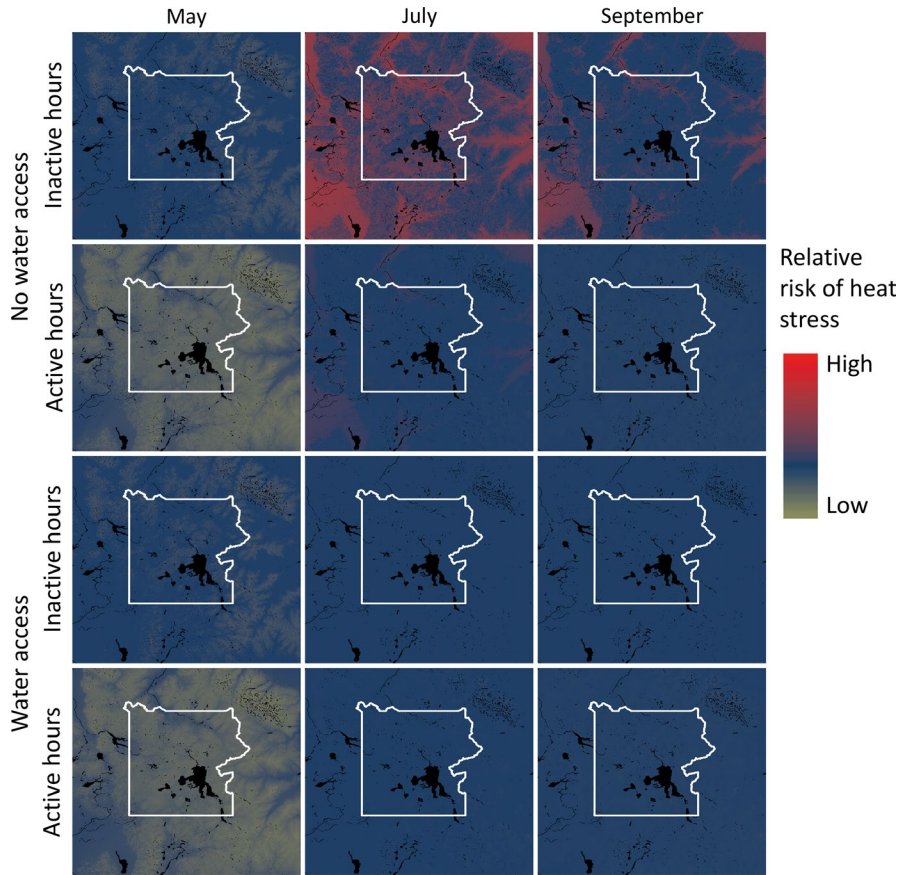


FIGURE 4 Spatiotemporal variation in the relative risk of heat stress, defined as the difference between predicted metabolic rate (kJ/day) and basal metabolic rate (BMR; see text for detailed explanation), for non-lactating female grizzly bears in Yellowstone National Park (YNP; outlined in white) and surrounding areas, USA. Permanent water bodies are overlaid in black. Inactive hours were defined as 11:00–16:59 and active hours were defined as 05:00–10:59 and 17:00–22:59 using empirical data on grizzly activity patterns in YNP (Appendix H). Bears were assumed to be sleeping between 23:00 and 05:00, and thus we excluded those hours from the analysis

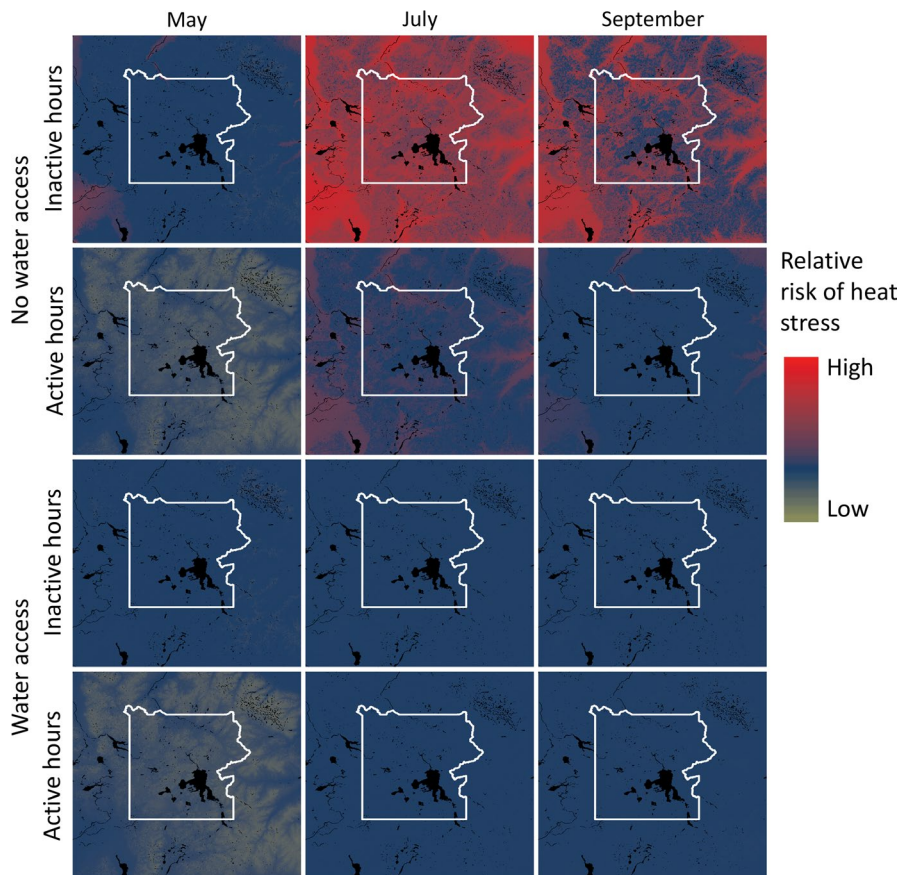


FIGURE 5 Spatiotemporal variation in the relative risk of heat stress, defined as the difference between predicted metabolic rate (kJ/day) and basal metabolic rate (BMR; see text for detailed explanation), for lactating female grizzly bears in Yellowstone National Park (YNP; outlined in white) and surrounding areas, USA. Permanent water bodies are overlaid in black. Inactive hours were defined as 11:00–16:59 and active hours were defined as 05:00–10:59 and 17:00–22:59 using empirical data on grizzly activity patterns in YNP (Appendix H). Bears were assumed to be sleeping between 23:00 and 05:00, and thus we excluded those hours from the analysis

We included landscape-scale predictions of the relative risk of heat stress as a covariate in our genetic programming model for modelling grizzly bear distribution. The most frequently recurring variable in distribution models for non-lactating female bears was elevation (100% of rules; Table 1). For lactating female bears, the most frequently recurring variables were elevation (100% of rules) and distance to major roads or highways (70.8% of rules). However, variables associated with the thermal environment occurred with greater frequency in rules for predicting the distribution of lactating (minimum daily temperature 54.2% of rules, maximum daily temperature 41.7% of rules, percent shade 33.3% of rules and relative risk of heat stress 33.0% of rules) than non-lactating (minimum daily temperature 16.7% of rules, maximum daily temperature 4.2% of rules, percent shade 12.5% of rules and relative risk of heat stress 4.2% of rules; Table 1) female bears. Overall predictive accuracy of distribution models was 77.3% and 77.5% for lactating and non-lactating female bears respectively (Appendix G).

4 | DISCUSSION

Our results support the hypothesis (H1) that grizzly bears in the Greater Yellowstone Ecosystem likely must invoke behavioural mechanisms of thermoregulation during summer, even at relatively low levels of activity. Empirical support for a strong relationship between temperature and bear activity across systems, however, has been mixed. For example, Sawaya et al. (2016) reported that American black bears, which are smaller bodied and ostensibly less heat-sensitive, regularly immersed themselves in water, and that this behaviour steadily increased in frequency as summer progressed, peaking when temperatures were highest. Similarly, Pigeon et al. (2016) reported that grizzly bears at higher latitudes in Canada increasingly favoured habitats with dense canopy cover as temperatures increased during summer. In contrast, McLellan and McLellan (2015) found that when foraging rewards were sufficient, grizzly bears remained active at air temperatures exceeding 30°C. These inconsistent results likely reflect the high degree of behavioural plasticity that has allowed grizzly bears to occupy a wide array of habitats and ecosystems in the northern hemisphere. Our analyses provide mechanistic insight into the importance of behavioural plasticity to large endotherms and suggest that energy allocation by female grizzly bears during summer can be constrained by the thermal environment.

Our hypothesis that lactating female bears are subject to greater thermal constraints on energy balance because of the increased heat generated by lactation (H2) also was supported by our simulations. Even at relatively low temperatures in early summer, lactating females were limited to lower levels of activity than their non-lactating counterparts, and temperature increases predicted under climate change exacerbated this trend. This result suggests that female grizzly bears may be faced with trade-offs in energy allocation that are consistent with predictions of the heat dissipation limit theory (Speakman & Król, 2010a) and with the generally slow life histories of large-bodied endotherms (Speakman & Król, 2010b). Indeed, our results indicate that the production of additional endogenous heat during lactation likely imposes constraints on the level of activity attainable by a

female bear (i.e. locations of active lactating females in YNP generally were limited to areas of low relative risk of overheating; Appendix H).

Access to water played an important role in reducing predicted costs of thermoregulation incurred by both lactating and non-lactating female grizzly bears during summer. Bears could seek shade in all of our simulations, and thus the frequent use of water by simulated bears when it was available suggests that shade alone was usually insufficient for maintaining homeothermy on warm days. Although bedding on cool substrate also reduced the predicted costs of thermoregulation, the benefit was not as pronounced as that of partial submergence in cool water. This result is likely a conservative estimate of the benefits of bed sites to bears in real systems, because the microclimatic conditions of actual bed sites may facilitate higher rates of cooling. For example, ambient temperature and shade availability in an actual bed site may differ substantially from conditions at BRECC that were used to parameterize Niche Mapper.

Our results are consistent with the hypothesis that grizzly bears are able to buffer themselves against the effects of high temperatures through behavioural thermoregulation. Indeed, during summer Yellowstone grizzly bears exhibit a distinct crepuscular pattern of activity in which they rest in beds that they dig down to mineral soil during the hottest hours of the day (Moe et al., 2007, Fortin, Ware, et al., 2013, Appendix I). Although this is an effective behavioural response under current climatic conditions, our analyses suggest that increasing temperatures associated with climate change may reduce the number of daily hours during which heat balance can be achieved without direct access to water for cooling, supporting our third hypothesis (H3). Bears are behaviourally adaptable and can accommodate temperature increases by extending crepuscular activity earlier and later in the active season and by further adjusting diel patterns of activity (e.g. by become increasingly nocturnal). Additional work is needed to determine how elastic these and other thermoregulatory behaviours are among grizzly bears. For example, it is unknown whether shifts in the timing or duration of foraging, or the need to increase time spent submerged in water, could alter energy budgets and affect growth and reproduction, and how such effects might manifest in population dynamics or demography.

The nature of predictions generated by Niche Mapper must be taken into consideration when interpreting our results. The model predicts metabolic rates at an hourly time step, which assumes that the model animal is sustaining the specified activity level for the entire hour. The ability of a bear to dramatically increase its activity for short periods (e.g. sprinting to capture a prey item) and then to subsequently recover is not accounted for. Thus, our results are most appropriately interpreted as estimates of the relative cost of activity at different times of the day and under different conditions (i.e. lactating vs. non-lactating, access to water or not, current vs. future climate).

Results from our spatiotemporal distribution analysis suggest that under current climatic conditions, variation in the thermal environment is not a more important predictor of grizzly bear distribution than other environmental factors, which does not support our fourth hypothesis (H4). Instead, our analysis showed that elevation and distance to roads were consistently more important predictors of the distribution of

female bears. This could be due in part to the relatively high amount of human activity in the Yellowstone ecosystem. Multiple studies have shown that grizzly bears avoid roads and human developments and that they will alter their behaviour in response to human activities (e.g. Boyce & Waller, 2003; Martin et al., 2010). Similarly, elevation is often negatively associated with human disturbance (Apps et al., 2004; Martin et al., 2010) and positively associated with two important food resources for grizzly bears in the summer and fall: whitebark pine nuts *Pinus albicaulis* and army cutworm moths *Euxoa auxiliaris* (Fortin, Schwartz, et al., 2013; French et al., 1994), which may help to explain the role of elevation in our modelling results. Although the thermal environment was not the dominant predictor of grizzly bear distributions in our genetic programming model, variables related to temperature did occur with greater relative frequency in the predictive rules for lactating than for non-lactating female bears. This supports our fifth hypothesis (H5) and suggests that variation in costs imposed by the thermal environment plays a greater role in dictating the behaviour of female bears when endogenous heat production increases during lactation. This result also is consistent with predictions of the heat dissipation limit theory (Król et al., 2003; Król & Speakman, 2003a, 2003b; Speakman & Król, 2010b) and may have important implications for population performance of grizzly bears. If capacity for heat dissipation is reduced when ambient air temperatures are high, female bears may be forced to allocate less energy to lactation as the climate warms (Król et al., 2003).

Our results also highlight the importance of access to water for thermoregulation. The availability of pools of cool water in which bears could partially submerge themselves increased the amount of habitat predicted to have a low relative risk of overheating for both non-lactating and lactating bears. Thus, access to water to submerge in makes a much greater portion of the landscape available to bears during the hottest parts of the year. Accordingly, the distribution of bears may sometimes be constrained to areas with water access, consistent with the hypothesis posed by Sawaya et al. (2016) for black bears in western Montana. Although regional predictions for the Yellowstone ecosystem suggest that precipitation may increase by up to 10% over the next century (IPCC, 2014), it is difficult to know to what degree any increase in water availability across the landscape might help to mediate the increased costs of thermoregulation imposed by warming temperatures. Understanding such trade-offs will be an important avenue for future research.

Algorithmic modelling relies on stochastic processes to identify patterns in data, and thus descriptive statements generated by this approach will vary with each run of the model. The accuracy of any given descriptive statement, however, is deterministic, and so consideration of many possible descriptive statements lends credibility to the relative importance of a single result. Our genetic programming model was designed to prioritize the interpretability of results; given the trade-off between accuracy and interpretability it is possible that a more accurate predictive result could have been obtained through additional tree complexity (i.e. greater height and more nodes) and runtime approaching infinity. However, the relatively high accuracies of our predictive statements suggest that our models were sufficiently optimized given the data that were used to fit them.

Our results have important implications for population performance of large, endothermic species in a warming climate. The potential for rising temperatures to directly constrain energy allocation to growth and reproduction by endotherms has not been evaluated for most species (Speakman & Król, 2010a), including grizzly bears. Yet, responses of endotherms to climatic variation are highly variable across taxa, and thus mechanistic, species-directed approaches will be critical for understanding and predicting the effects of climate change on distribution and performance of wildlife populations (Fuller et al., 2016). Our results suggest that climatic modulation of costs imposed by the thermal environment likely is an important driver of behaviour and energetics in large endotherms and that relative importance of the thermal environment to endotherm ecology is likely to increase as the climate continues to warm.

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AUTHORS' CONTRIBUTIONS

S.A.R., R.A.L. and C.T.R. conceived the ideas and designed the study; S.A.R., T.R.R., T.S., W.P.P. and P.D.M. developed the methodologies; S.A.R., C.T.R., T.S., F.T.v.M. and M.A.H. collected the data; S.A.R. analysed the data; S.A.R. and R.A.L. wrote the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data used in this manuscript are either (a) publicly available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.3tx95x6f2> (Rogers et al., 2020), or (b) are precluded from public distribution by the National Parks Omnibus Management Act of 1998, Title II, Sec 207 (e.g. grizzly bear GPS location data).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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