

**Climatic Constraints on Energy Balance, Behavior and Spatial
Distribution of Grizzly Bears**

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Authorization to Submit Thesis

This Thesis of Savannah A. Rogers, submitted for the degree of Master of Science with a Major in Bioinformatics and Computational Biology and titled "Climatic Constraints on Energy Balance, Behavior and Spatial Distribution of Grizzly Bears" has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Although the influence of environmental variation on energy balance of endotherms is well understood, the degree to which climate directly constrains energy available for reproduction in large mammals has received comparatively little attention. We used a combination of biophysical and algorithmic modeling to examine the impact of temperature variation on rates of metabolism and water loss of lactating and non-lactating female grizzly bears, *Ursus arctos*. Our goal was to understand the conditions in which warm temperatures constrain activity (both timing and intensity) and to quantify the relative importance of regulatory behaviors for maintaining heat balance. We used the mechanistic modeling software Niche Mapper to predict energetic costs incurred by female bears in early and late summer under current (measured) climatic conditions, as well as under conditions predicted by the IPCC (i.e., 2.5°-C increase in mean temperature). When bears were allowed access to “bathtubs” (i.e., pools of cool water) to facilitate cooling they were able to maintain homeothermy under a wider range of conditions throughout the summer, especially under simulated climate warming. The relative benefit of bathtubs was greater for lactating females because of the additional endogenous heat generated by lactation. Our results suggest that behavioral mechanisms for minimizing costs of thermoregulation are likely to play an important role in the ecology of grizzly bears at the southern extent of their range under current conditions, and that increasing temperatures have the potential to constrain energy allocated to reproduction by grizzly bears. To explore this possibility further we used an algorithmic modeling approach to evaluate the relative influence of costs imposed by the thermal environment on the spatial distribution of female grizzly bears. We developed a Genetic Program to predict the relative contribution of a suite of environmental variables to

the distribution of lactating and non-lactating female bears in the Greater Yellowstone Ecosystem Grizzly Bear Recovery Zone. Although our model results did not indicate that variation in the thermal environment is a more important determinant of grizzly bear distribution than other environmental factors under current climatic conditions, they did show that spatiotemporal variation in costs of thermoregulation have a greater influence on the distribution of lactating than non-lactating female bears. This result is consistent with predictions of the Heat Dissipation Limit Theory and has important implications for the distribution and performance of grizzly bear populations in the GYE as the earth's climate continues to warm.

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Dedication

This thesis is dedicated to anyone who has welcomed a wide-eyed undergraduate into the world of research.

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Chapter 1: Climatic Constraints on Energy Balance and Behavior of Grizzly Bears

Abstract

Although the influence of environmental variation on energy balance of endotherms is well understood, the degree to which climate directly constrains energy available for reproduction in large mammals has received comparatively little attention. We used a biophysical model to examine the impact of temperature variation on rates of metabolism and water loss of lactating and non-lactating female grizzly bears, *Ursus arctos*. Our goal was to understand the conditions in which warm temperatures constrain activity (both timing and intensity), and to quantify the relative importance of regulatory behaviors for maintaining heat balance. We used the mechanistic modeling software Niche Mapper to predict energetic costs incurred by female bears in early and late summer under current (measured) climatic conditions, as well as under conditions predicted by the IPCC (i.e., 2.5° C increase in mean temperature). When bears were allowed access to “bathtubs” (i.e., pools of cool water) to facilitate cooling, they were able to maintain homeothermy under a wider range of conditions throughout the summer, especially under simulated climate warming. The relative benefit of bathtubs was greater for lactating females because of the additional endogenous heat generated by lactation. Our results suggest that behavioral mechanisms for minimizing costs of thermoregulation are likely to play an important role in the ecology of grizzly bears at the southern extent of their range under current conditions, and that increasing temperatures have the potential to constrain energy allocated to reproduction by grizzly bears.

Introduction

Climate directly affects energy balance of endothermic animals by determining the costs (i.e., metabolic rate and evaporative water loss) of maintaining homeothermy (Porter et al. 2000, 2002). Although the magnitude of those costs varies widely among species and habitats, the Heat Dissipation Limit Theory (HDLT; Speakman and 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 byproduct of normal metabolic processes (McNab 2002), 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 thus the amount of energy that can be devoted to growth, reproduction or activity is constrained by the capacity of endotherms to dissipate that heat, even if energy supplies are effectively unlimited (Król and Speakman 2003a, b; Król et al. 2003; Speakman and Król 2010a,b).

Because endogenous heat production increases markedly during gestation and lactation (Speakman and McQueenie 1995, Urison and Buffenstein 1995, Bowers 2009), climate may impose greater constraints on energy expenditure by female than male mammals. 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 reproductive processes have important implications for female fitness, and thus population performance, in a warming climate. Increasing the environmental heat load experienced by female mammals will likely decrease their ability to

devote energy to reproduction, thereby decreasing milk production and subsequent offspring body mass and/or litter size (Johnson and Speakman 2001, Król and Speakman 2003a,b; Król et al. 2003).

In addition to constraints imposed on reproductive investment, high environmental temperatures may limit the timing or duration of physical activity. Like gestation and lactation, activity increases the production of endogenous heat that must subsequently be dissipated, and previous studies have demonstrated that high environmental temperatures can constrain activity of some mammals (e.g., Belovsky 1981, Creel et al 2016, Hall and Chalfoun 2018). Such constraints are likely to become even more pronounced across a wider variety of taxa as average global temperatures continue to rise.

Grizzly bears (*Ursus arctos*) are an iconic mammal in western North America. Yet, management of grizzly bears is often fraught with controversy, as is evidenced by the 2017 decision by the U.S. Fish and Wildlife Service to remove grizzly bears from the endangered species list, followed by the quick reversal of that decision by a federal judge in 2018. As part of the process for considering grizzly bears for delisting, the U.S. Fish and Wildlife service evaluated the relative contribution of food resources (i.e., quality, availability and distribution of key food resources) to the stability of grizzly populations in the lower 48 States. In contrast, the potential for climate change to influence behavior and/or performance of grizzly populations by increasing costs of thermoregulation and activity has received little attention (although some researchers have examined the relationship between temperature and activity levels; MacHutchon et al. 1998, Fortin et al. 2013, McLellan and McLellan 2015). As the climate warms, bears may experience new constraints on behavior, such as the need to limit diurnal activity to reduce exposure to solar radiation (Ward et al. 1999).

Understanding how much of an increase in temperature is necessary to begin imposing such constraints is critical for future conservation and management of grizzly bears.

Large-bodied animals like grizzly bears have smaller surface-area-to-volume ratios and thicker boundary layers than their smaller-bodied counterparts. As a result, larger animals are more limited in their ability to dissipate heat. This biophysical first principle suggests that as temperatures continue to rise, grizzly bears may be forced to invest more resources (i.e., energy and water) into regulating their body temperature, especially near the southern extent of their range. Although some of this regulation can be accomplished physiologically, bears also have the ability to alter their behavior, particularly as they move across large landscapes. Behavior often serves as an important buffer against environmental variation (Huey et al. 2003, Long et al. 2014), and large mammals can regulate their exposure to costs imposed by the thermal environment through a variety of behavioral mechanisms. One example of such behavior in bears is the use of “bear bath tubs” (i.e., pools of cool water) to lower their body temperature during summer months in the Greater Yellowstone Ecosystem (Sawaya et al. 2017). Nevertheless, the relative importance of behavioral thermoregulation in grizzly bears is poorly understood. Understanding how and to what degree environmental temperature constrains behavior and energy balance of grizzly bears could provide important insights into potential responses of grizzly bears to climate warming.

Our objective was to understand the extent to which climate (i.e., environmental temperature) constrains behavior (e.g., timing and duration of daily activity) and energy balance of grizzly bears by determining costs of thermoregulation across a range of temperatures and activity levels. 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 will be forced to invoke behavioral and/or 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 especially when environmental temperatures peak during summer; (H2) Because of the additional heat loads created by lactation, female grizzly bears that are lactating will be subject to greater energetic constraints than non-lactating females under the same environmental conditions; (H3) Warming temperatures predicted by models of climate change over the next century will increase costs of thermoregulation and limit the hours of the day during which female grizzly bears can successfully thermoregulate.

Methods and Materials

Thermodynamic modeling

We estimated costs of thermoregulation experienced by grizzly bears in a variety of different scenarios using Niche Mapper (Porter et al. 2002, Porter and Mitchell 2006, Natori and Porter 2007). Niche Mapper is a mechanistic model based on biophysical first principles that estimates the metabolic and hydric costs of maintaining homeothermy under a given set of environmental conditions by solving the energy balance equation (Porter and Gates 1969) for the species being modeled (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 model animal and its environment to predict hourly rates of water loss and metabolism necessary to maintain a constant body temperature (Porter et al. 2002, Natori and Porter 2007, Huang et al. 2013, Long et al. 2014).

The microclimate submodel uses empirical data supplied by the user to calculate hourly profiles of temperature, wind speed, humidity, and solar radiation 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 this average day is representative of all days within the user-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 environmental model has been widely tested and validated across a range of ecosystems (Porter et al. 1973, Mitchell et al. 1975, Fuentes and Porter 2013, Kearney et al. 2014).

We parameterized the microclimate model using data from a HOBOware weather station and data logger placed along the perimeter of the captive grizzly enclosure at the Washington State University Bear Research, Education, and Conservation Center (WSUBRECC) during summer (May through September), 2018. The weather station recorded temperature, wind speed, and relative humidity at 5-min intervals. We obtained data on daily cloud cover from a public database hosted by WeatherUnderground (<https://www.wunderground.com/>). Daily minima and maxima for each variable were averaged over the course of each week during the summer, and those average extrema were then used by the microclimate model to calculate profiles for each variable during an average day of that week. In addition, to estimate costs of thermoregulation in a warming climate, we re-parameterized the microclimate submodel with temperature data that aligned with predictions of the IPCC PCP8.5 model for the middle of the 21st century (i.e., we added 2.5°C to our empirical measurements of average high and low temperatures).

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, etc.; Natori and Porter 2007; Long et al. 2014) in concert with vegetation characteristics and the output from the microclimate model; together, output from the endotherm and microclimate submodels define the animal's thermal environment (Appendix A). In order to solve the energy balance equation for the animal at each time step the animal is allowed to thermoregulate both behaviorally and physiologically. The model assumes a "best-case scenario," and first allows the animal to perform a series of behavioral responses (i.e., seeking shade) before resorting to physiological responses (i.e., panting or sweating) that invoke a metabolic or water cost. The model allows the animal to engage in thermoregulatory behaviors as soon as net heat gain would result in increased internal temperature without intervention. When energy and/or water must be expended to maintain heat balance, these costs are reported as hourly estimates by the model. Hourly estimates are then integrated into an estimate of the total costs incurred by the animal at the location being modeled during an average day. Multipliers of basal metabolic rate can also be used to account for different levels of physical or reproductive activity (e.g., lactation).

To parameterize the endotherm model we obtained pelt and body measurements from 5 adult female bears at the WSUBRECC. We measured hair length and fur depth with a digital caliper. Fur density (hairs per cm^2) 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 5 subsamples from the total shaved sample. We then weighed each subsample to establish the relationship between subsample weight and number of hairs, and estimated the total number of hairs in the full shaved sample as a function of its weight.

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 100x magnification and then measuring the width using ImageJ software (available from the National Institute of Health Research Services Branch; <https://imagej.nih.gov/>). We measured pelt reflectivity across a range of wavelengths (350 -2500 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). 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 five captive adult grizzly bears housed at the WSUBRECC. 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/h; 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 basal metabolic rate (BMR) to account for varying levels of activity) 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/h (Craighead et al. 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 modeling an active bear (inactive bear = BMR, active bear = 1.56 x BMR).

To investigate the relative importance of “bath tubs” as a strategy for thermoregulation by bears, we conducted several simulations in which bears were given the option to submerge up to 100% of their body and 80% of their neck in cool (ground-water temperature ~14°C) water to achieve heat balance through convective and conductive cooling. To evaluate the importance of bathtubs relative to other behavioral cooling mechanisms, access to shade (up to 100%) was included in the comparative simulations. We also examined the impact of lactation on heat balance of female bears by using an additional energetic multiplier (1.52 x BMR; Gittleman 1989) to account for heat generated at peak lactation.

We used Niche Mapper to compare costs of thermoregulation among bears during summer (May – September) in the following scenarios: 1) lactating females at rest versus active, and with or without access to bathtubs; 2) non-lactating females at rest versus active, and with or without access to bathtubs; and 3) the same scenarios described in (1) and (2) with a 2.5°C increase in temperature minima and maxima to simulate the effects of climate warming.

Results

During early summer (mid-May), predicted metabolic rates of non-lactating, inactive female bears were unaffected by diel variation in environmental temperature (i.e., bears were able to maintain heat balance without the need to thermoregulate behaviorally or physiologically; **Error! Reference source not found.**). In contrast, to keep from overheating

during the hottest hours of the day (roughly 10:00 to 16:00 hrs), lactating females required water (i.e., access to “bath tubs”) to thermoregulate behaviorally (Fig. 1-1); access to shade alone was insufficient for cooling. During late summer inactive bears of both reproductive classes were predicted to overheat during some portion of the day in the absence of water, even with access to shade (Figure 1-2). However, when bathtubs were available for thermoregulation, both lactating and non-lactating female bears were able to achieve heat balance (Figure 1-2).

In both early and late 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. In early summer, non-lactating females were able to successfully dissipate the heat produced by a high level of activity (i.e., travel at 3.6 km/hr; 1.56 x BMR) during only 16 hours of the day (mostly at night and during crepuscular hours; **Error! Reference source not found.**) even when water was available for cooling. Access to water was still important, however, and allowed non-lactating females in early summer to maintain ~85.8% of the target activity level without overheating during the remaining 8 hours of the day (1.29 x BMR; **Error! Reference source not found.**). The importance of water for thermoregulation was even greater for non-lactating females during late summer. In the absence of water, non-lactating females were predicted to overheat during the hottest four hours of the day, but were able to sustain up to 84.6% of the target activity level during those hours when water was available for cooling (1.28 x BMR; Fig. 1-2).

Lactating female bears were unable to sustain a high level of activity during any hour of the day in early or late summer. The maximum sustainable level of activity for lactating females during either period was 89.3% of the target rate (1.34 x BMR; Figs. 1-1 and 1-2),

which suggests that the increased heat produced by traveling at 3.6 km/h cannot be effectively dissipated by lactating female bears in early or late summer, regardless of access to water (**Error! Reference source not found.** and Figure 1-2). Access to water did, however, facilitate a higher level of activity (1.12 x BMR in early summer and 1.10 x BMR in late summer), and effectively prevented overheating during the hottest part of the day in both early and late summer (Figs. 1-1 and 1-2).

For both reproductive classes, temperature increases predicted under climate change reduced the number of hours in which bears could achieve heat balance while inactive by up to 55.1% (range = 0.2 – 55.1%; Fig. 1-3). However, the effect of climate warming on time available for activity was modulated by the availability of water for cooling (Fig. 1-3). In the absence of water, 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 1-3). However, when water was available to facilitate cooling, non-lactating females were able to achieve heat balance 24 hrs/day throughout the summer by thermoregulating behaviorally under current climate conditions, and during most of the summer even under future climate conditions (Figure 1-3).

Constraints imposed by climate warming were more pronounced for lactating than for non-lactating female bears. Although access to water increased the proportion of the day during which heat balance could be achieved by up to 37.5% under current climate conditions and by up to 54.2% in future climate conditions, lactating females were still at risk of overheating for up to 9 hrs/day during a large portion of the summer (roughly from July 9 to September 3).

Discussion

Access to water played an important role in reducing predicted costs of thermoregulation for both lactating and non-lactating female bears during summer. Bears were allowed to 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 rarely sufficient for maintaining thermoneutrality on warm days. These results support our first hypothesis that bears will frequently be forced to invoke behavioral mechanisms of thermoregulation during summer, even at relatively low levels of activity. In addition, our results are consistent with observed patterns of behavior in bears, particularly near the southern extent of their range. For example, Sawaya (2016) reported that American black bears regularly immersed themselves in water sources to thermoregulate, and that this behavior 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 favored habitats with denser canopy cover as temperatures increased during summer. Our analyses provide mechanistic insight into these observations, and suggest that energy allocation by female grizzly bears during summer may already be constrained to some degree by climate.

Our second hypothesis, that lactating female bears are subject to greater climatic constraints on energy balance because of the increased heat generated by lactation, also was supported. 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 suggests that female grizzly bears may be faced with tradeoffs in energy allocation that are consistent with predictions of the Heat Dissipation Limit Theory (Speakman and Król 2010a), and with the

generally slow life-histories of large-bodied endotherms (Speakman and Król 2010b).

Indeed, our results indicate that the production of additional endogenous heat during lactation likely imposes serious constraints on the level of activity attainable by a female bear. Such constraints could reduce population performance not only by limiting investment in reproduction, but also by limiting the ability of females to optimize (with respect to factors other than the thermal environment) their movements and distribution on the landscape, particularly when summer temperatures are at their zenith.

As global temperatures continue to rise, direct effects of climate on bears are likely to become even more pronounced. Our results suggest that although grizzly bears will be able to buffer themselves behaviorally against such effects to some extent, female bears near the southern extent of their range may already be approaching the limits of those abilities. In our models, increasing temperatures predicted under climate change decreased the proportion of the day during which heat-balance was achievable for both non-lactating and lactating female bears, supporting our third hypothesis. A reduction in the mean number of daily hours when activity is possible may have important consequences for grizzly bears, which are largely diurnal and crepuscular during summer even under current climatic conditions (Fortin et al. 2013). For example, fewer hours available for foraging could reduce energy intake, further exacerbating climatic constraints on growth and reproduction.

The nature of predictions generated by Niche Mapper must be carefully considered 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).

Our results have important implications for population performance of grizzly bears 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 and 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 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 grizzly bear behavior and energetics, and that relative importance of the thermal environment to grizzly bear ecology is likely to increase as the climate continues to warm.

Literature Cited

- Belovsky, G.E. (1981) Optimal activity times and habitat choice of moose. *Oecologia*, **48**, 22-30.
- Bowers, S., Gandy, S. Anderson, B., Ryan, P, and Willard, S. (2009) Assessment of pregnancy in the late-gestation mare using digital infrared thermography. *Theriogenology*, **72**, 372-377.
- Butler, P.J., West, N.H. and Jones, D.R. (1977) Respiratory and cardiovascular responses of the pigeon to sustained, level flight in a wind-tunnel. *Journal of Experimental Biology*, **71**, 7-26.
- Craighead, F.C. (1976) Grizzly bear ranges and movement as determined by radiotracking in Pelton, M.R., Lentfer, J.W., and Folk, G.E. Bears – their biology and management. *IUCN Publication*, **40**, 97-109.
- Creel, S., Creel, N.M., Creel, A.M., and Creel, B.M. (2016) Hunting on a hot day: effects of temperature on interactions between African wild dogs and their prey. *Ecology*, **97**, 2910-2916.
- Fortin, J.K. (2011) Niche separation of grizzly (*Ursus arctos*) and American black bears (*Ursus americanus*) in Yellowstone National Park. Dissertation, Washington State University, Pullman, Washington.
- Fortin, J.K., Ware, J.V., Jansen, H.T., Schwartz, C.C., and Robbins, C.T. (2013) Temporal niche switching by grizzly bears but not American black bears in Yellowstone National Park. *Journal of Mammalogy*, **94**, 833-844.
- Fuentes, M. and Porter, W. (2013) Using a microclimate model to evaluate impacts of climate change on sea turtles. *Ecological modelling*, **251**, 150 – 157.
- Fuller, A., Mitchell, D., Maloney, S.K. and Hetem, R.S. (2016) Towards a mechanistic understanding of the responses of large terrestrial mammals to heat and aridity associated with climate change. *Climate Change Responses*, **3**, online.
- Gittleman, J.L. (1989) Carnivore behavior, ecology, and evolution volume 1. Cornell University Press, Ithaca, New York.
- Hall, L.E. and Chalfoun, A.D. (2018) Behavioural plasticity modulates temperature-related constraints on foraging time for a montane mammal. *Journal of Animal Ecology*, **00**, 1-13.

- Huang, S., Chiou, C., Lin, T., Tu, M., Lin, C., and Porter, W.P. (2013) Future advantages in energetics, activity time, and habitats predicted in a high-altitude pit viper with climate warming. *Functional Ecology*, **27**, 446-458.
- IPCC,(2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
- Huey, R.B., Hertz, P. E., and Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *The American Naturalist*, **161**, 357 – 366.
- Johnson, M.S. and Speakman, J.R. (2001) Limits to sustained energy intake V. Effect of cold-exposure during lactation in *Mus musculus*. *Journal of Experimental Biology*, **204**, 1967–1977.
- Kearney, M. R., Shamakhy, A., Tingley, R., Karoly, D.J., Hoffmann, A.A., Briggs P.R., and Porter, W.P. (2014) Microclimate modelling at macro scales: a test of a general microclimate model integrated with gridded continental-scale soil and weather data. *Methods in Ecology and Evolution* **5**, 273 – 286.
- Khadka, K.K. and James, D. A. (2017) Modeling and mapping the current and future climatic-niche of endangered Himalayan musk deer. *Ecological Informatics*, **40**, 1 – 7.
- Król, E. and Speakman, J.R. (2003a) Limits to sustained energy intake VI. Energetics of lactation in laboratory mice at thermoneutrality. *Journal of Experimental Biology*, **206**, 4255–4266.
- Król, E. and Speakman, J.R. (2003b) Limits to sustained energy intake VII. Milk energy output in laboratory mice at thermoneutrality. *Journal of Experimental Biology*, **206**, 4267–4281.
- Król, E., Johnson, M.S. and Speakman, J.R. (2003) Limits to sustained energy intake VIII. Resting metabolic rate and organ morphology of laboratory mice lactating at thermoneutrality. *Journal of Experimental Biology*, **206**, 4283–4291.
- Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., and Kie, J. G. (2014) Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecological Monographs*, **84**, 513 – 532.

- Long, R.A., Bowyer, R.T., Porter, W.P., Mathewson, P., Monteith, K.L., Findholt, S.L., Dick, B. L., and Kie, J. G. (2016) Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape. *Oecologia*, **181**, 709 – 720.
- MacHutchinson A.G., Himmer S., Davis H., and Gallagher M. (1998) Temporal and spatial activity patterns among coastal bear populations. *Ursus*, **10**, 539–546.
- McLellan M.L. and McLellan B.N. (2015) Effect of Season and High Ambient Temperature on Activity Levels and Patterns of Grizzly Bears (*Ursus arctos*). *PLoS ONE* **10**, 1-14.
- McNab, B.K. (2002) The physiological ecology of vertebrates: a view from energetics. Cornell University Press, Ithaca, New York.
- Mitchell, J., Beckman, W., Bailey, R., and Porter, W. (1975) Microclimatic modeling of the desert in deVries, D.A. and Afgan, N.H. Heat and mass transfer in the biosphere, Part 1, 275 – 286, Halsted Press, Wiley, NY.
- Natori, Y., and Porter, W.P. (2007) Model of Japanese serow (*Capricornis crispus*) energetics predicts distribution on Honshu, Japan. *Ecological Applications*, **17**, 1441–1459.
- Pigeon, K.E., Cardinal, E., Stenhouse, G.B. and Cote, S.D. (2016) Staying cool in a changing landscape: the influence of maximum daily ambient temperature on grizzly bear habitat selection. *Oecologia*, online.
- Porter, W. P., and Gates, D. M. (1969) Thermodynamic equilibria of animals with environment. *Ecological Monographs*, **39**, 227–244.
- Porter, W. P., and Mitchell, J. W. (2006) Method and system for calculating the spatial-temporal effects of climate and other environmental conditions on animals. U.S. Patent 7,155,377 in December, 2006. <https://www.google.com/patents/US7155377>
- Porter, W.P., Budaraju, S., Stewart, W.E., and Ramankutty, N. (2000) Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. *American Zoologist*, **40**, 597 – 630.
- Porter, W.P., Mitchell, J.W., Beckman, W.A., and DeWitt, C.B. (1973) Behavioral implications of mechanistic ecology. *Oecologia*, **13**, 1 – 54.
- Porter, W.P., Munger, J. C., Stewart, W. E., Budaraju, S., and Jaeger, J. (1994) Endotherm energetics: from a scalable individual-based model to ecological applications. *Australian Journal of Zoology*, **42**, 125–162.

- Porter, W.P, Ostrowski, S., and Williams, J. G. (2010) Modeling animal landscapes. *Physiological and Biochemical Zoology*, **83**, 705 – 712.
- Porter, W.P., Sabo, J.L., Tracy, C.R., Reichman, O.J., and Ramankutty, N. (2002) Physiology on a landscape scale: plant– animal interactions. *Integrative and Comparative Biology*, **42**, 431– 453.
- Post, E., Langvatn, R., Forchhammer, M.C. and Stenseth, N.C. (1999) Environmental variation shapes sexual dimorphism in red deer. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 4467– 4471.
- Renecker, L A. and Hudson, R.J. (1986) Seasonal energy expenditures and thermoregulatory responses of moose. *Canadian Journal of Zoology*, **64**, 322 – 327.
- Sawaya, M.A., Ramsey, A.B. and Ramsey, P.W. (2016) American black bear thermoregulation at natural and artificial water sources. *Ursus*, **27**, 129-135.
- Shine, C.L., Penberthy, S., Robbins, C.T., Nelson, O.L., and McGowan, C.P. (2015) Grizzly bear (*Ursus arctos horribilis*) locomotion: gaits and ground reaction forces. *Journal of Experimental Biology*, **218**, 3102-3109.
- Speakman, J.R. and Król E. (2010a) Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, **79**, 726 – 746.
- Speakman, J.R. and Król, E. (2010b) The heat dissipation limit theory and evolution of life histories in endotherms—time to dispose of the disposable soma theory? *Integrative and Comparative Biology*, **50**, 793–807.
- Speakman, J.R. and McQueenie, J. (1995) Limits to sustained metabolic rate: the link between food intake, basal metabolic rate, and morphology in reproducing mice, *Mus musculus*. *Physiological Zoology*. **69**, 746-769.
- Stockwell D.R.B. and Noble, I.R. (1992) Induction of sets of rules from animal distribution data: a robust and informative method of data analysis. *Mathematics and Computers in Simulation*, **33**, 385 – 390.
- Urison, N.T. and Buffenstein, R.B. (1995) Metabolic and body temperature changes during pregnancy and lactation in the naked mole rat (*Heterocephalus glaber*). *Physiological Zoology*, **68**, 402-420.

Ward, S., Rayner, J.M., Moller, U., Jackson, D.M., Nachtigall, W. and Speakman, J.R.
(1999) Heat transfer from starlings *Sturnus vulgaris* during flight. *Journal of Experimental Biology*, **202**, 1589–1602.

Ward, S., Moller, U., Rayner, J.M.V., Jackson, D.M., Nachtigall, W. and Speakman, J.R.
(2004) Metabolic power of European starlings *Sturnus vulgaris* during flight in a wind tunnel, estimated from heat transfer modelling, doubly labelled water and mask respirometry. *Journal of Experimental Biology*, **207**, 4291–4298.

Figures

Figure 1-1. Predicted hourly metabolic rates (W) from Niche Mapper for lactating and non-lactating female bears at low (BMR) and high ($1.52 \times \text{BMR}$) activity levels during an average day from May 7 to May 13, 2018 at the Washington State University Bear Research, Education, and Conservation Center in Pullman, Washington, USA. Blue lines represent predicted metabolic rates when bears have access to “bath tubs” (i.e., pools of $\sim 14^\circ\text{C}$ water) for cooling, and black lines represent predicted rates in the absence of bath tubs. Basal metabolic rate is denoted by a dashed grey line. Predicted metabolic rates that drop into the shaded portion of the graph below BMR denote conditions in which the bear is predicted to overheat. The second Y-axis denotes the percentage of the target metabolic rate for sustaining high activity levels ($1.52 \times \text{BMR}$) that is attainable in the modeled scenario.

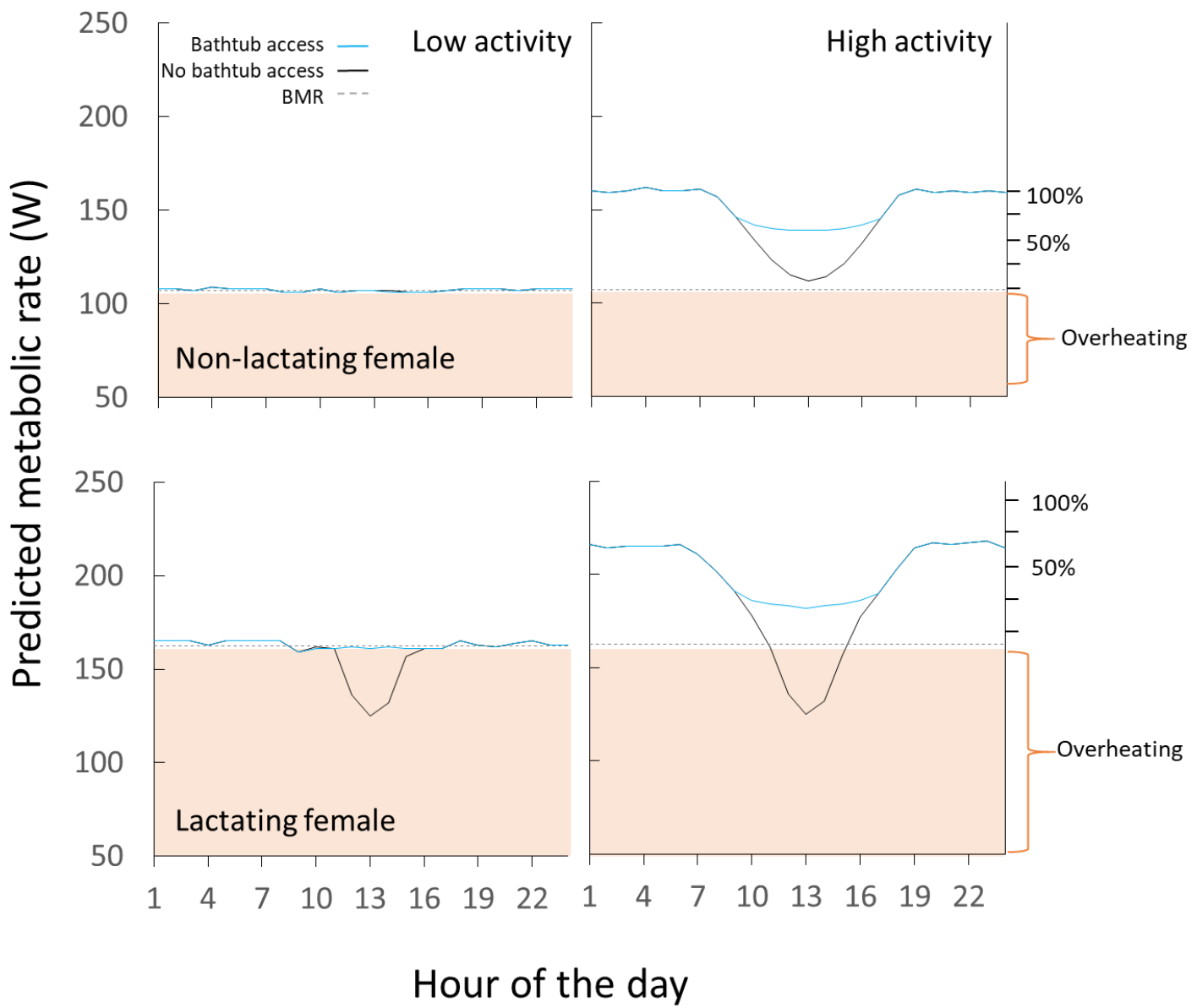


Figure 1-2. Predicted hourly metabolic rates (W) from Niche Mapper for lactating and non-lactating female bears at low (BMR) and high ($1.52 \times \text{BMR}$) activity levels during an average day from September 27 to October 3, 2018 at the Washington State University Bear Research, Education, and Conservation Center in Pullman, Washington, USA. Blue lines represent predicted metabolic rates when bears have access to “bath tubs” (i.e., pools of $\sim 14^{\circ}\text{C}$ water) for cooling, and black lines represent predicted rates in the absence of bath tubs. Basal metabolic rate is denoted by a dashed grey line. Predicted metabolic rates that drop into the shaded portion of the graph below BMR denote conditions in which the bear is predicted to overheat. The second Y-axis denotes the percentage of the target metabolic rate for sustaining high activity levels ($1.52 \times \text{BMR}$) that is attainable in the modeled scenario.

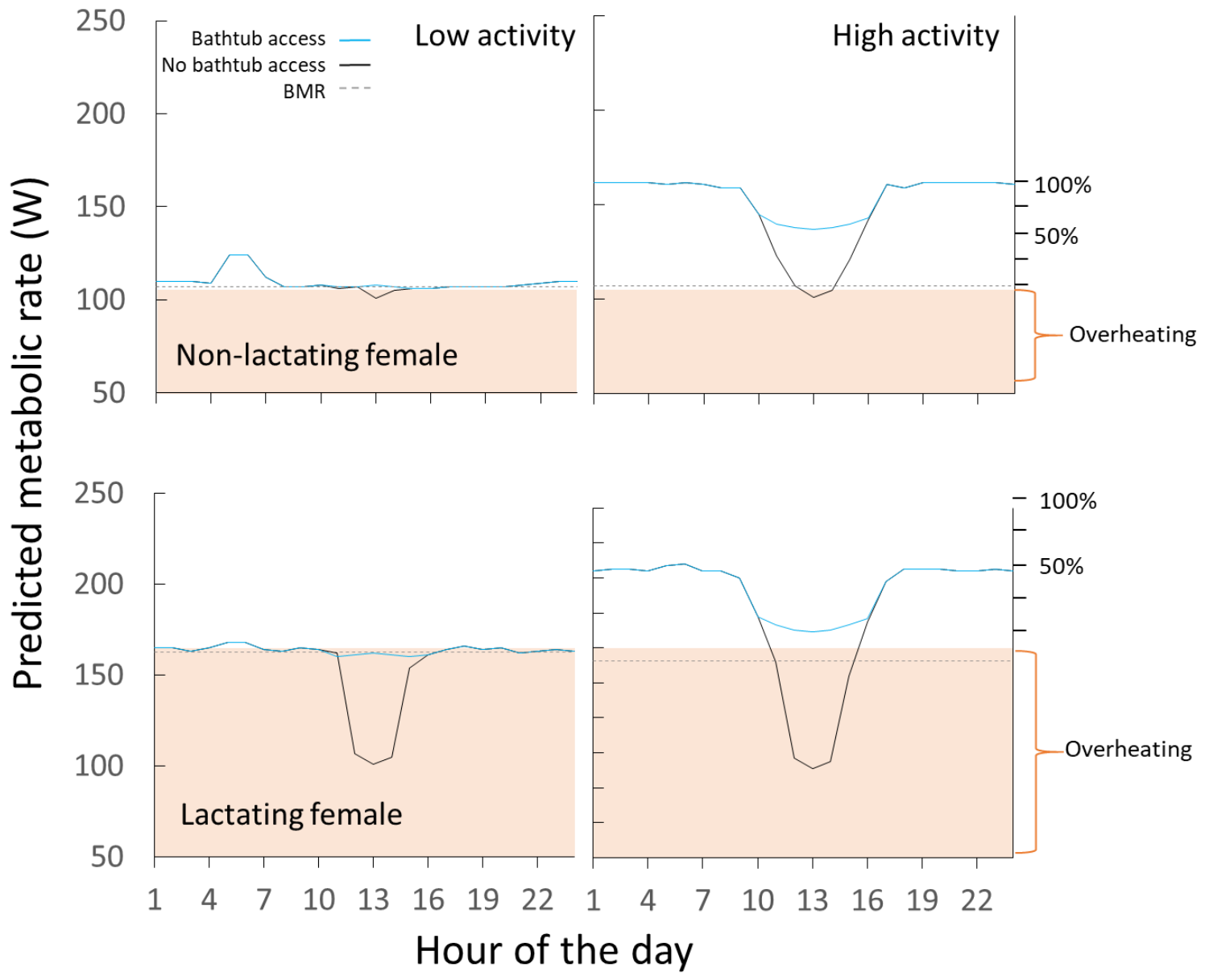
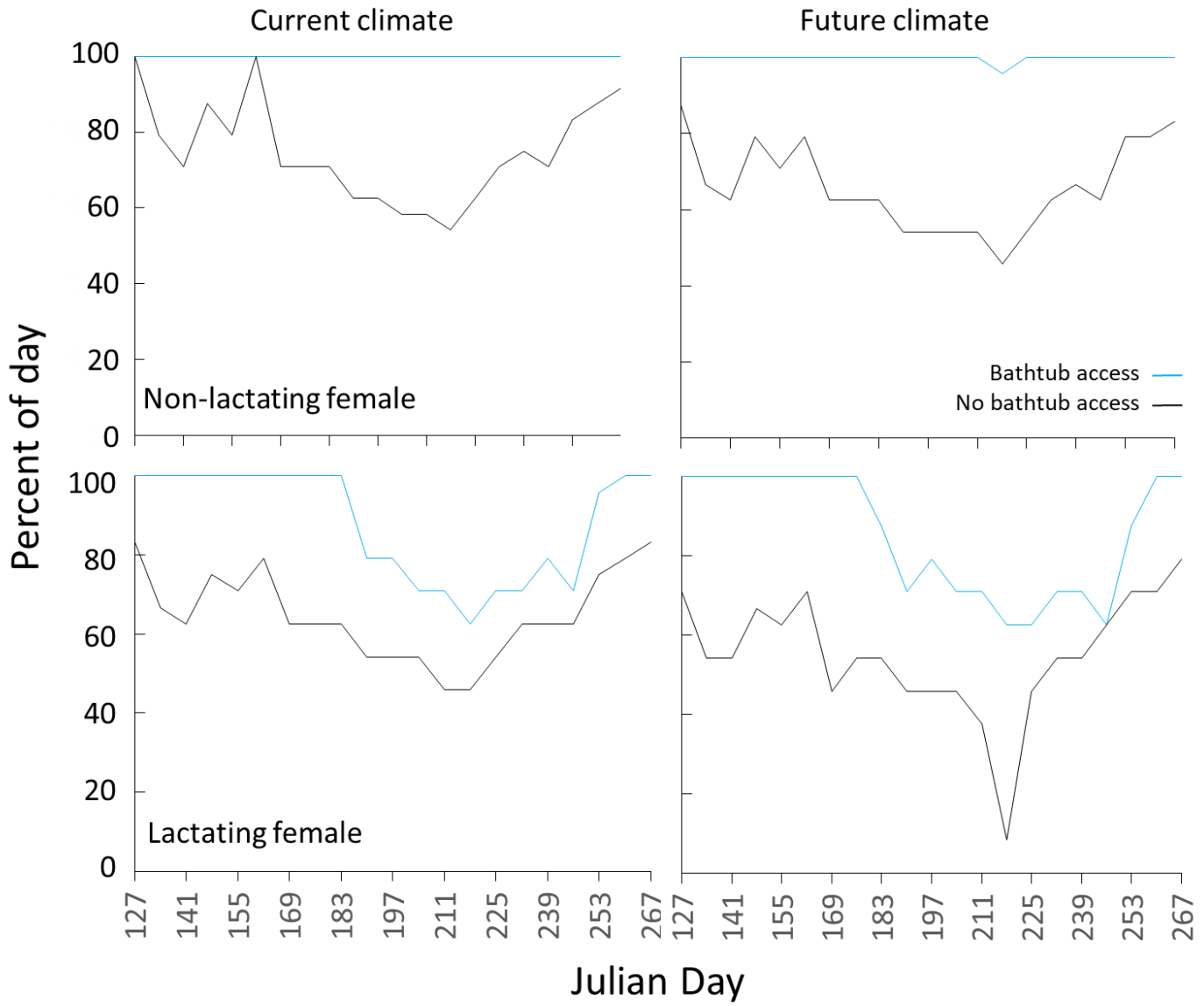


Figure 1-3. Predicted percentage of the day between May 7 and October 3 during which inactive non-lactating and lactating female bears are able to achieve heat balance in both current climate conditions and under the 2.5°-C temperature increase predicted by the IPCC R8.5 over the next 100 years. Blue lines represent predicted percentage of the day that bears are able to achieve heat balance when they have access to “bath tubs” (i.e., pools of ~14°C water) for cooling, and black lines represent predicted percentage of the day that they can achieve heat balance in the absence of bath tubs.



Chapter 2: The Relative Impact of Thermal Environment on the Distribution of Female Grizzly Bears

Abstract

Species distributions are predicted to change as global temperatures warm, but the relative importance of the various mechanisms driving those changes (e.g., direct versus indirect effects of climatic variation on energy balance) remains poorly understood. We used a combination of biophysical and algorithmic modeling to examine the impact of temperature variation on the distribution of lactating and non-lactating female grizzly bears, *Ursus arctos*, in the Greater Yellowstone Ecosystem Grizzly Bear Recovery Zone, USA. Our goal was to evaluate the relative importance of spatiotemporal variation in costs of thermoregulation as a determinant of grizzly bear distribution. We used the mechanistic modeling software Niche Mapper to map thermoregulatory costs across the landscape, and then incorporated those cost predictions, along with a suite of other environmental variables, into a Genetic Program that determined the relative importance of each variable for predicting the distribution of GPS-collared bears. Although environmental variables such as elevation and human disturbance were important for predicting the presence of both lactating and non-lactating female bears, our model did not identify variation in the thermal environment as a strong driver of female bear distribution. However, variation in the thermal environment was relatively more important for predicting the distribution of lactating than non-lactating female bears, likely due to the increase in endogenous heat production associated with lactation. Our results are consistent with other studies that have highlighted the role of human disturbance in determining the distribution of bears, and with predictions of heat dissipation limit theory in

that variation in the thermal environment appears to impose greater constraints on the ecology of lactating than non-lactating female grizzly bears. Relative importance of the thermal environment to female bears in general, but especially to lactating females, is likely to increase as the climate continues to warm, which may have important implications for performance of grizzly bears in the Recovery Zone.

Introduction

The earth's climate is warming at an unprecedented rate (Braconnot et al. 2012, IPCC 2013, IPCC 2014), and understanding the effects of climate change on ecosystem processes is one of the most pressing challenges faced by modern ecologists. One of the most striking effects of climate change on terrestrial ecosystems is the alteration of species distributions (Pimm 2008, Heller and Zavaleta 2009, Moritz and Agudo 2013), and such effects have been demonstrated extensively across multiple taxa (Jetz et al. 2007, Colwell et al. 2008, Garcia et al. 2012, Alamgir et al. 2015, Aryal et al. 2016, Mukul et al. 2019). Climate determines the fundamental niche of endothermic species at the most basic level by dictating the conditions in which it is possible to maintain homeothermy (Hutchinson 1957, as discussed in Kearney and Porter 2004). Accordingly, climate change can fundamentally alter the potential of a landscape to provide suitable habitat for a species if temperature extrema or other climatic variables begin to drift outside the boundaries of a species' fundamental niche.

The use of niche modeling as a tool for predicting how species' distributions will respond to environmental change has increased dramatically in recent years (Brown et al 2016, Martinez-Minaya 2018). Critics of this approach contend that the correlative nature of most niche models, although informative in the context of current conditions, limits the

ability of those models to accurately forecast responses to future climate scenarios (Dawson et al. 2011, Araujo and Peterson 2012) and provides little insight into the potential for behavioral, plastic, or genetic responses to climate change (Davis et al. 1998, Jeschke et al. 2008). Mechanistic niche models help to overcome these limitations by explicitly considering the capacity of species to buffer themselves against negative effects of climate change through behavioral, morphological, and/or physiological means (Kareiva et al. 1993, Helmuth et al. 2005, Kearney and Porter 2009).

One important mechanism by which climate change directly affects the distributions of endothermic animals is by determining the energetic 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, 2002). The Heat Dissipation Limit Theory (HDLT; Speakman and Król 2010) posits that the capacity of endotherms to dissipate heat imposes a greater constraint on energy allocation to growth and reproduction than their ability to harvest energy from the environment. Endotherms generate considerable heat as a byproduct of normal metabolic processes (McNab 2002), and to effectively maintain a stable core temperature this heat must be dissipated to the environment. Furthermore, endogenous heat production increases during reproduction (i.e., gestation and lactation) and activity (e.g., traveling or foraging), and thus high environmental temperatures may constrain the ability of endotherms to invest energy in those functions even if energy supplies are effectively unlimited (Porter and Gates 1969; Król and Speakman 2003a, b; Król et al. 2003; Porter and Kearney 2009; Speakman and Król 2010a, b). For these reasons, climate warming may have more pronounced effects on female than male endotherms, which has important implications for population dynamics and performance in a warming climate.

The implications of HDLT are particularly salient for large mammals in the face of a warming climate. In contrast to smaller species, large-bodied mammals can accumulate high internal heat loads because their smaller surface-area-to-volume ratios and thicker boundary layers limit rates of convective heat and mass loss to the environment (Porter and Gates 1969, Porter and Kearney 2009). This biophysical first principle suggests that large animals may be forced to invest disproportionately more resources into regulating body temperature as environmental temperatures continue to rise.

One large mammal of conservation concern is the grizzly bear (*Ursus arctos*). Current grizzly bear populations in North America range from northern Canada and Alaska (latitude 74°) through the northernmost part of the western conterminous United States, with isolated populations as far south as Yellowstone National Park (latitude 43°) (although historic distributions ranged as far south as Mexico [latitude 22°] and included much of the western United States; COSEWIC 2012). Like most large mammals, grizzly bears have slow life histories; female grizzlies typically reproduce for the first time between 4 and 7 years old, and the average interbirth interval is 2.6 years (litter size is usually two cubs; Ferguson and McLoughlin 2000; Schwartz et al. 2006). Although the inverse relationship between body size and the pace of life is well known, Speakman and Król (2010b) recently suggested that limits to heat dissipation may be the mechanism underlying this trend; if endotherms are constrained by their maximum ability to dissipate heat, and heat loss is fundamentally surface-based, then the low surface-area-to-volume ratio of large mammals likely limits their ability to dissipate the additional heat generated by reproduction, leading to a slower life history (Speakman and Król 2010b).

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., grizzly bears have been shown to alter their behavior to avoid high-traffic roads; Northrup et al. 2012; Apps et al. 2006). To date, however, no studies have used mechanistic niche models to evaluate the relative importance of spatiotemporal variation in costs of thermoregulation as a driver of grizzly bear distributions. The goal of our study was to evaluate the influence of energetic costs imposed by climate on the distribution of grizzly bears in the Yellowstone National Park Grizzly Bear Recovery Zone (GRZ) relative to other factors already known to influence bear distribution. In accordance with that goal we test the following hypotheses: (H1) The landscape-scale distribution of grizzly bears in the GRZ will be influenced more by spatiotemporal variation in the thermal environment than by habitat type or human disturbance, particularly during the warmest summer months; (H2) 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 females.

Methods and Materials

Study area

We modeled potential determinants of grizzly bear distribution in Yellowstone National Park (hereafter YNP) and the surrounding Grizzly Bear Recovery Zone (hereafter

GRZ; latitude 44, longitude -110; **Error! Reference source not found.**; U.S. Fish and Wildlife Service 1993). The GRZ surrounds YNP and includes Grand Teton National Park, in combination with both National Forest and private lands. In 2007 the grizzly bear population in the GRZ was estimated to number between 490 and 629 individuals, of which 275 were estimated to be females with cubs of the year (Haroldson 2008, Kamath 2015). The population is estimated to be near its carrying capacity based on survival rates of young and the proportion of the population comprised by adult bears (Haroldson 2008). 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 at the Parker Ponderosa/Gus's Gulch weather station in West Yellowstone (elevation 2,032 m) in summer (May through August) was 84° F in 2007 and 81° F in 2008. Elevations in the park range between 1,610 and 3,462 meters.

Animal location data

To train and validate models of grizzly bear distribution in the GRZ we used GPS collar data from 14 resident (i.e., $\geq 95\%$ of locations occurred within YNP) female bears obtained during summers of 2007 and 2008. Additional details on capture and handling of grizzly bears can be found in Peck et al. (2017) and were based on methods developed by Blanchard (1983). All animal handling was approved by the Institutional Animal Care and Use Committee at the University of Idaho (protocol #IACUC-2018-21).

Energetics modeling: Niche Mapper

We estimated costs of thermoregulation experienced by grizzly bears in a variety of different scenarios and habitats using Niche Mapper (Porter et al. 2002, Porter and Mitchell 2006, Natori and Porter 2007). Niche Mapper is a mechanistic model based on biophysical

first principles that estimates the metabolic and hydric costs of maintaining homeothermy under a given set of environmental conditions by solving the energy balance equation (Porter and Gates 1969, Mathewson and Porter 2013) for the species being modeled (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 model animal and its environment to predict hourly rates of water loss and metabolism necessary to maintain a constant body temperature at a specific location and time (Porter et al. 2002, Natori and Porter 2007, Huang et al. 2013, Long et al. 2014). A landscape-scale permutation of Niche Mapper can be used to predict costs of thermoregulation for each pixel in a landscape during a user-specified temporal window.

The microclimate submodel uses climate data supplied by the user to calculate hourly profiles of air temperature, wind speed, humidity, and solar radiation 2 meters 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 this 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 environmental model has been widely tested and validated across a range of ecosystems (Porter et al. 1973, Natori and Porter 2007, Huang et al. 2013).

To parameterize the microclimate model for the GRZ 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 the

period 1981 to 2010 (Daly et al. 2008). Cloud cover data (percentages) were obtained from the EarthEnv datasets (<https://www.earthenv.org/cloud>), which use twice-daily MODIS satellite images integrated over 15 years (2000 to 2014) to generate monthly average cloud cover estimates (Wilson and Jetz 2016). We estimated relative humidities 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 (<https://www.mrlc.gov/data/nlcd-2011-usfs-tree-canopy-cartographic-conus>; Wickham et al. 2014). We used percent canopy cover as a measure of 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.

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, etc.; Natori and Porter 2007; Mathewson et al. 2016, Long et al. 2014) in concert with vegetation characteristics and the output from the microclimate model; together, output from the endotherm and microclimate submodels define the animal's thermal environment (Table 1). In order to solve the energy balance equation for the animal at each time step the animal is allowed to thermoregulate both behaviorally and physiologically. The model assumes a "best-case scenario," and first allows the animal to perform a series of behavioral responses (i.e., seeking shade) before resorting to physiological responses (i.e., panting or sweating) that invoke a metabolic or water cost. When energy and/or water must be expended to maintain heat balance, these costs are reported as hourly estimates by the model. Hourly estimates are then integrated into an estimate of the total costs incurred by the animal at the

location being modeled during an average day. Multipliers of basal metabolic rate can also be used to account for different levels of physical or reproductive activity (e.g., lactation).

To parameterize the endotherm model we obtained pelt and body measurements from 5 adult female bears at the Washington State University Bear Research, Education, and Conservation Center (hereafter WSUBRECC). We measured hair length and fur depth with a digital caliper. Fur density (hairs per cm^2) 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 5 subsamples from the total shaved sample. We then weighed each subsample to establish the relationship between subsample weight and number of hairs, and estimated the total number of hairs in the full shaved sample as a function of its weight. 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 100x magnification and then measuring the width using ImageJ software (available from the National Institute of Health Research Services Branch; <https://imagej.nih.gov/>). We measured pelt reflectivity across a range of wavelengths (350 -2500 nm) using an ASD portable spectrophotometer and integrated the resulting curve to estimate total pelt reflectivity. All measured parameters were averaged across individuals within each sex, and additional parameters were obtained from the literature (Appendix 1).

To investigate the relative importance of “bath tubs” as a strategy for thermoregulation by bears, we conducted several simulations in which bears were given the option to submerge up to 100% of their body and 80% of their neck in cool (~14°C) water to achieve heat balance. We also examined the impact of lactation on heat balance of female bears by using an additional energetic multiplier (1.52 x BMR; Gittleman 1989) to account for heat generated at peak lactation.

At the landscape scale, Niche Mapper conducts simulations on a pixel-by-pixel basis. For each pixel, the microclimate submodel conducts simulations based on environmental conditions specified by the user for that location and time. The microclimate model assumes the animal occupies the center of the pixel, and the endotherm submodel is then run for each pixel. Spatiotemporally explicit model predictions are assembled into a raster to generate a map of the energy cost landscape (Porter et al. 2002, Long et al. 2014, 2016, Zhang et al. 2018), with the value for each pixel representing the total predicted cost of the animal remaining at each location over the course of the average day.

Additional predictors of grizzly distribution

To evaluate relative importance of the thermal environment as a driver of grizzly bear distribution in the GRZ, we obtained data on several additional covariates with demonstrated potential to influence grizzly bear behavior and distribution. As a measure of human occupancy we used the 2010 U.S. Census Bureau Home Density layer (<http://www.census.gov/geo/maps-data/data/tiger-data.html>) and the calculated distance to major roads and highways. 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-land-cover-conterminous-united-states>), 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 was obtained at a resolution 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 used the Normalized Difference Vegetation Index (calculated from Landsat images of peak greenness) to quantify spatial variation in greenness in the GRZ from June 15 – July 15 in 2013 and 2015 (<https://earthengine.google.com/datasets/>).

Genetic Program Analysis

To evaluate relative importance of the thermal environment as a determinant of grizzly bear distribution we used a Genetic Programming model (Koza 1996) that was conceptually grounded in the Genetic Algorithm for Rule-set Prediction (GARP). GARP models predict species' distributions by iteratively improving a rule set applied to empirical data on species presence (Stockwell et al. 1992). This method is uniquely suited to ecological modeling due to its ability to explore and make predictions from noisy, high-dimensional, and discontinuous datasets, even with no background knowledge of the system, and it typically outperforms multivariate analyses with these types of data. Our Genetic Program expanded on GARP with a slightly more complicated design. Rules were defined as the range of possible values for a variable (see “rule nodes” in Fig 2-4) and were combined into unions and/or intersections (see “relation nodes” in Fig 2-4) to form a single descriptive statement that was represented within the program as a tree structure made up of nodes (see “individual” in Fig 2-4). The descriptive statement was then tested for accuracy in predicting grizzly bear presence on the landscape using a combination of known presence data (i.e., GPS collar locations) and pseudo-absence data (background sampling). Each descriptive

statement was then treated as an “individual” within a list of such statements, which together comprised the “population.” The accuracy of each descriptive statement served as the measure of its “fitness”. The entire population was then iteratively subjected to a “reproduction” event in which the most fit individuals (i.e., descriptive statements, see Fig 2-4) reproduced to form new individuals through crossover and mutation (descriptive statements traded rules and individual rules/linkages were stochastically altered) to form a new population. Over many successive generations, a best individual emerged, resulting in a descriptive statement that was maximally accurate for predicting grizzly bear presence, and facilitating direct interpretation of the relative importance of each covariate in the context of the role played by that covariate in the final rule set. Evolutionary parameters for the algorithm are detailed in Appendix 2.

We partitioned our data to facilitate comparison of the influence of different environmental covariates across reproductive classes (lactating versus non-lactating female) and through time (months of the summer, May through September). Background data were generated across space as well as across time.

Model Exploration

To estimate significance of each parameter, we ran the Genetic Program 15 times and calculated the percentage of occurrences of each parameter in the final rules for each best individual for each population. Because the nature of an algorithmic analysis is stochastic, standard statistical measures of significance for the method do not exist. We conducted a series of validation analyses of our Genetic Program, including comparison with three standard analytical approaches used for binary classification analyses; logistic regression, linear discriminant analysis, and quadratic discriminant analysis.

Results

Predicted spatiotemporal variation in costs of thermoregulation experienced by grizzly bears at the landscape scale differed markedly between lactating and non-lactating females (Figs. 2-2 and 2-3). We used predicted metabolic rates from Niche Mapper as a measure of the relative probability of a bear overheating at some point during the day. The relative probability of overheating increased during the hottest parts of the summer (e.g., July; Figs 2-2 and 2-3). Importantly, however, when bears were allowed access to water to cool behaviorally, relative probabilities of overheating were greatly reduced. 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 regardless of whether water was available for cooling.

Because bears in the GRZ do, in fact, have access to water for cooling (Sawaya et al. 2016), we used the predicted cost maps from Niche Mapper in which water was assumed to be available as covariates in our Genetic Program for predicting grizzly bear distribution. The final descriptive statement evolved by our Genetic Program indicated that the most important predictors of the distribution of non-lactating female bears were elevation (elevations between 2,266 and 2,696 meters were most predictive of presence) and/or a combination of elevation and distance to roads or highways (locations with elevation between 2,266 and 2,749 m and distances between 3,522 and 27,881 m from roads were most predictive of presence; Table 2-1). The predictors in the most accurate description of the distribution of lactating female bears were a combination of elevation and minimum daily temperature (locations with elevations between 2,184 and 2,495 m and with mean minimum temperatures between -2° and 5.5° C were most predictive of presence) and/or distance to streams or rivers

(locations with distances between 2,995 and 3,896 m from streams and rivers were most predictive of presence; Table 2-1). The accuracy of these descriptive statements for predicting presence of non-lactating and lactating grizzly bears in 2007-2008 was 74.56% and 81.93%, respectively (Table 2-1).

The relative importance of covariates, thermal and otherwise, for predicting bear distribution differed between non-lactating and lactating females. The most frequently occurring variables in distribution models for non-lactating female bears were distance to roads (28.6% of rules) and elevation (25.7 % of rules; Table 2-2). For lactating female bears the most frequently occurring variables were elevation (28.4% of rules) and variables associated with air temperature (minimum daily temperature 8.1% of rules, maximum daily temperature 16.2% of rules, and predicted metabolic rate 10.8% of rules; Table 2-2). Land cover type was included in 8.6% of rules for predicting the distribution of non-lactating bears, but in only 4.1% of rules for predicting the distribution of lactating bears (Table 2-2). NDVI did not occur in any predictive rules (Table 2-2).

The Genetic Program consistently had a higher confusion-matrix accuracy than traditional modeling approaches (Table 2-3). A logistic regression model with all available covariates returned accuracies of 71.18% for lactating bears and 63.39% for non-lactating bears (Table 2-3). The linear discriminant analysis had accuracy rates of 64.95% and 63.18% for lactating and non-lactating females, respectively, and predictive accuracy of the quadratic discriminant analysis was 73.55% and 58.91% for lactating and non-lactating females, respectively (Table 2-3).

Discussion

Our results suggest that under current climatic conditions, spatiotemporal variation in the thermal environment is not a more important predictor of grizzly bear distribution than other environmental factors, which does not support our first hypothesis. Instead, our analysis showed that distance to roads and elevation were consistently more important predictors of the distribution of female bears. This could be due in part to the large amount of human disturbance in the Yellowstone ecosystem. Multiple studies have shown that grizzly bears avoid roads and human developments, and that they will alter their behavior in response to human disturbance (e.g., Boyce and 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*) in the Yellowstone ecosystem (French et al. 1994, Fortin et al. 2013), which may help to explain the role of elevation in our modeling results.

Although the thermal environment was not the dominant predictor of grizzly bear distributions in our Genetic Program, variables related to temperature did occur with greater relative frequency in the predictive rules for lactating than for non-lactating female bears. Indeed, the best descriptive statement evolved by our model for lactating female bears included maximum temperature as a predictor, whereas the best descriptive statement for non-lactating female bears did not. This supports our second hypothesis and suggests that variation in costs imposed by the thermal environment plays a greater role in dictating the distribution of female bears when endogenous heat production increases during lactation. This result is consistent with predictions of the heat dissipation limit theory (Król and

Speakman 2003a,b; Król et al 2003; Speakman and Król 2010b), which predicts that activity of lactating female endotherms is limited by their ability to dissipate the additional endogenous heat produced during lactation. Moreover, these results 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).

Temperatures in the GRZ are predicted to increase by 2.5°C (IPCC 2014) over the next century as a result of climate change. Given that the thermal environment already has a greater influence on the distribution of lactating than non-lactating female bears, warming temperatures could force lactating females to make more pronounced tradeoffs in habitat selection. For example, as temperatures increase, lactating female bears may be forced to utilize habitat with lower-quality food resources if that habitat provides reduced thermoregulatory costs, a pattern already reported in herbivores (Long et al. 2016). Such tradeoffs may prove especially costly during late summer, when temperatures often peak and food resources are critical for bears in hyperphagia.

Our results also highlight the importance of bathtubs to female bears in the GRZ. The availability of bathtubs dramatically increased the amount of habitat predicted to have a low relative probability of overheating for both non-lactating and lactating bears. Thus, the use of bathtubs could make a much greater portion of the landscape available to bears during the hottest parts of the year. This suggests that the distribution of bears may sometimes be limited to areas where bathtubs are present, a hypothesis that is consistent with previous findings for black bears in the area (Sawaya et al. 2016).

Two advantages of using a Genetic Program are 1) that it requires no model tuning, and 2) that accuracy is not influenced by collinearity among variables. Thus, there are no limitations on which or how many variables can be considered. A Genetic Program also eliminates variables that have a negative impact on the response, so it does not require comparison of multiple permutations of covariates. Instead, it can complete the entire selection and tuning process with the entire suite of variables. The predictive strength of our model was higher than that of more traditional statistical approaches for predicting animal distributions. Although it is possible that a more accurate logistic regression, LDA, or QDA could be developed for our data, fitting such models would require greater attention to variable selection, collinearity, overdispersion, and other assumptions that do not apply to our algorithmic approach. A Genetic Program is also equally suitable for multi-model or highly clustered data because of its ability to link rules together with an “or” relation, and it often produces a relatively accurate result with no preliminary segregation of data.

One limitation of our approach is that our analyses did not capture the specific times during which bears were physically present at the locations being modeled. Average daily energetic costs (i.e., the output from Niche Mapper) may not be as effective a predictor of all bear locations over the course of a month as hourly estimates of cost. Indeed, other studies have reported diel variation in bear distribution and activity (Moe et al. 2007, Pigeon et al. 2016). Nevertheless, because our models included the full range of variation in energetic cost, the relative importance of energetic cost should remain consistent independent of time.

Algorithmic modeling 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 program was designed to prioritize interpretability of results; given the tradeoff 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, comparisons of our model with traditional approaches suggest our models were sufficiently optimized given the data that were used to fit them.

Our results have important implications for population performance of grizzly bears in a warming climate. The potential for rising temperatures to constrain grizzly bear distributions by limiting energy available for growth and reproduction has not been previously evaluated. 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 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 plays an important role in grizzly bear behavior and energetics, and that relative importance of the thermal environment to grizzly bear ecology is likely to increase as the climate continues to warm.

Figures

Figure 2-1. Map of our study area, which encompassed the Grizzly Bear Recovery Zone (yellow boundary) and Yellowstone National Park (red boundary) in the western U.S.A.

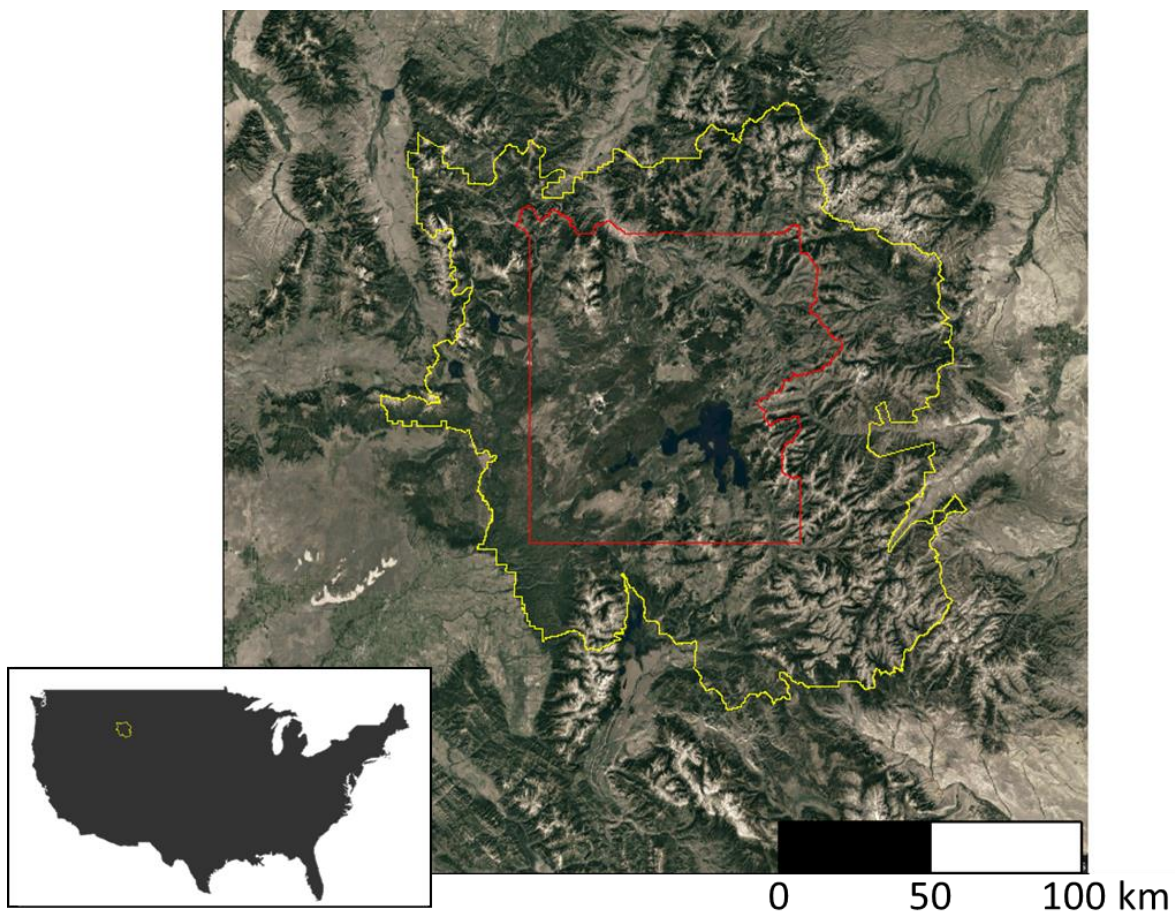


Figure 2-2. Map of predicted metabolic rates (kJ/d) necessary for non-lactating female bears to maintain homeothermy in the Grizzly Bear Recovery Zone, U.S.A., including Yellowstone National Park (YNP; outlined in black). Basal Metabolic Rate (BMR) is denoted by a white bar on the legend. As predicted metabolic rates drop below BMR the relative probability of overheating during at least some portion of the day is predicted to increase.

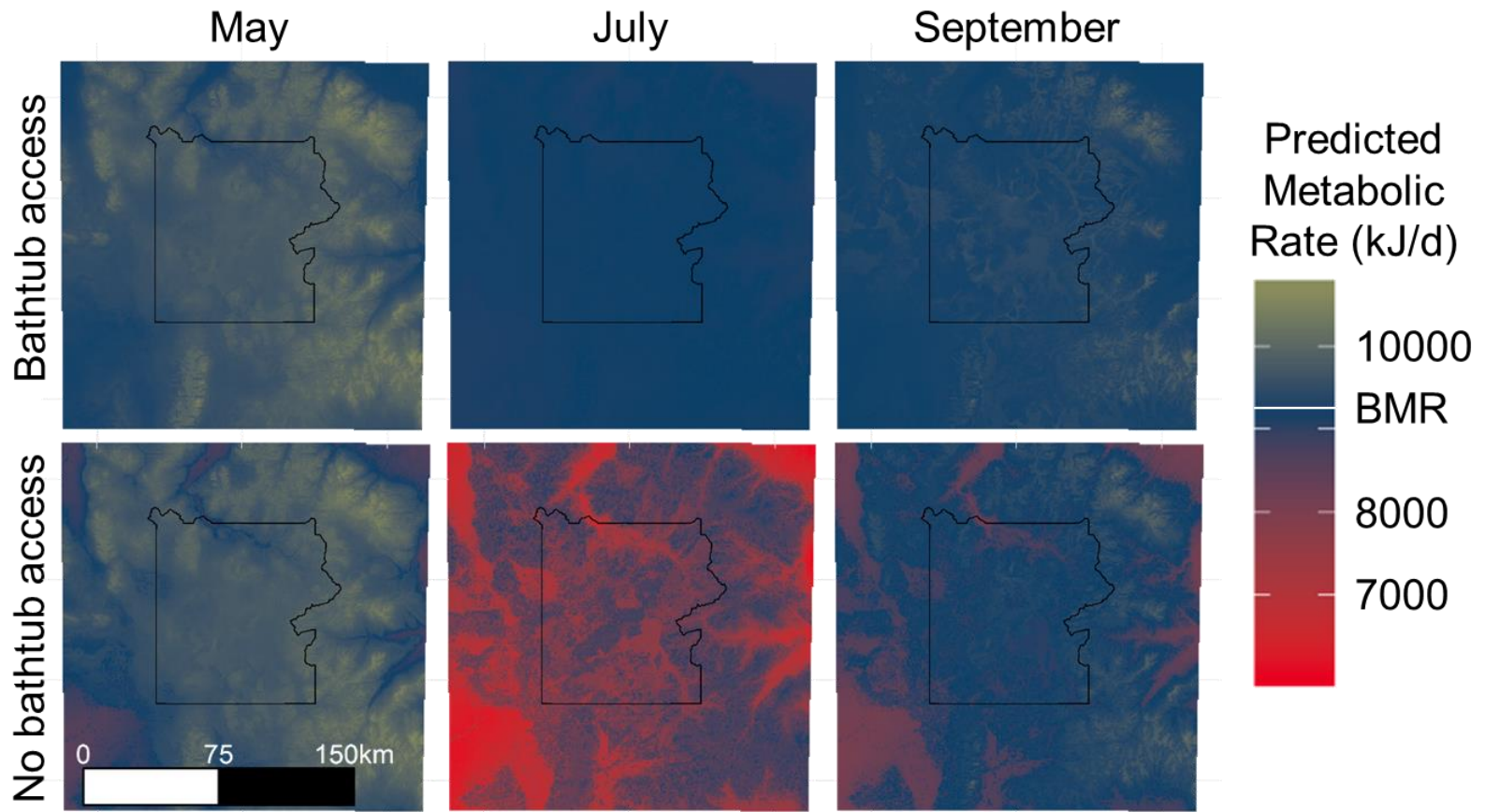


Figure 2-3. Map of predicted metabolic rates (kJ/d) necessary for lactating female bears to maintain homeothermy in the Grizzly Bear Recovery Zone, U.S.A., including Yellowstone National Park (YNP; outlined in black). Basal Metabolic Rate (BMR) is denoted by a white bar on the legend. As predicted metabolic rates drop below BMR the relative probability of overheating during at least some portion of the day is predicted to increase.

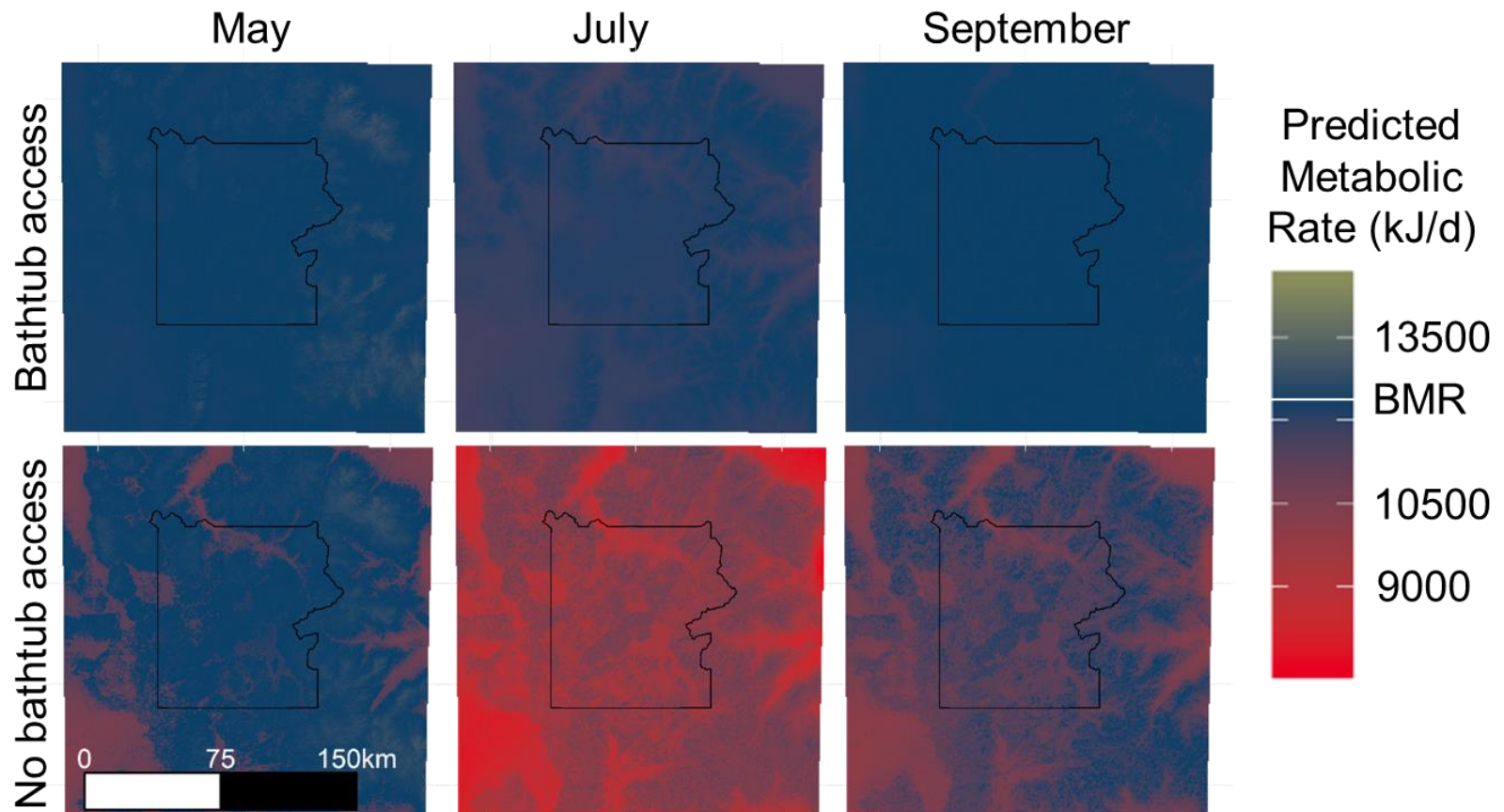
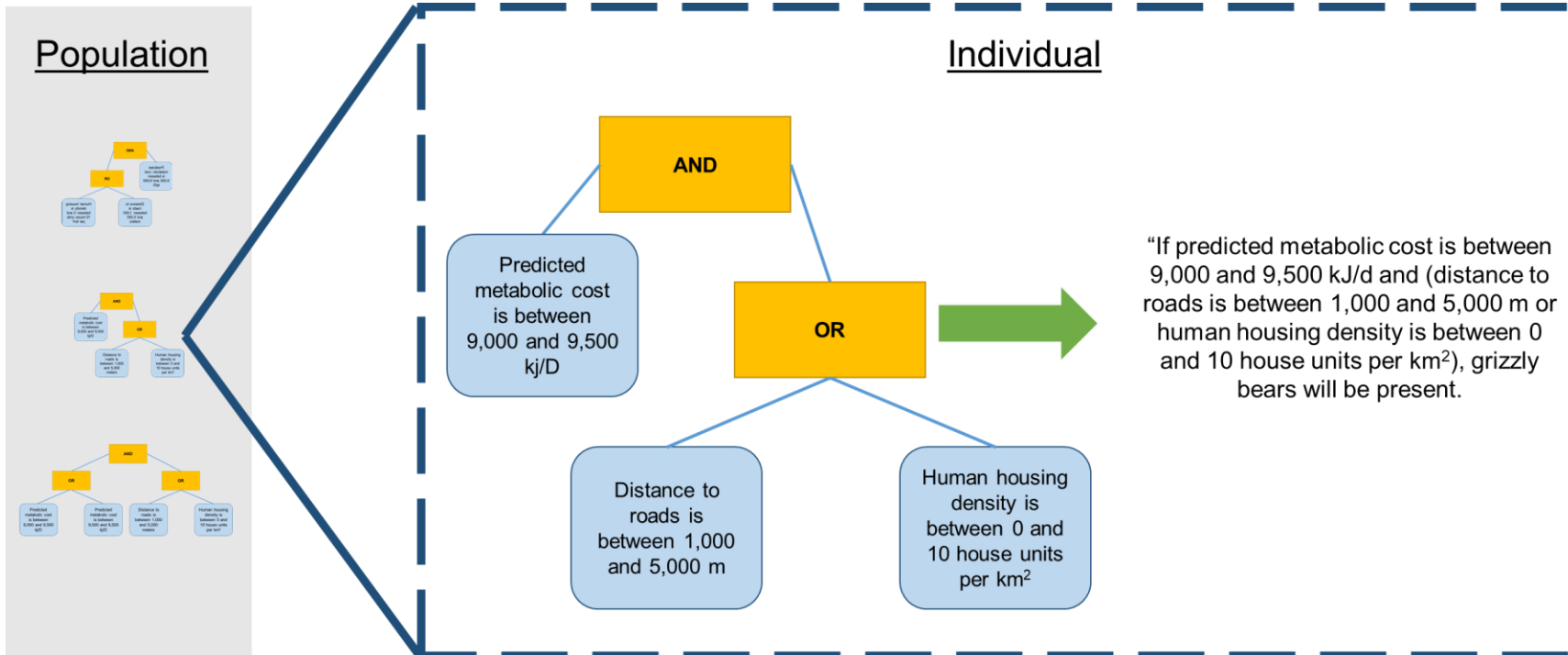


Figure 2-4. Example of a descriptive statement tree (“individual”) made up of rule and relation nodes. Rule nodes are represented by blue boxes and relation nodes are represented by yellow boxes. The interpretation of the tree is given on the right side of the figure. Possible relation nodes include “AND,” “OR,” “AND NOT,” and “OR NOT.” Possible rule nodes include all possible ranges of user supplied variables (variables for this analysis are detailed in Chapter 2 methods).



Tables

Table 2-1. Final descriptive statements evolved from the Genetic Program for predicting the distributions of lactating and non-lactating female grizzly bears in the Grizzly Bear Recovery Zone, U.S.A., including Yellowstone National Park, and their corresponding accuracies^a.

Lactating	Non-lactating
<p>If (elevation is between 2,184 and 2,495 m and daily minimum temperature is between -2° and 5.5° C) or distance to streams or rivers is between 2,995 and 3,896 m, lactating female bears are present.</p>	<p>If elevation is between 2,266 and 2,696 m or (distance to roads or highways is between 3.522 and 27.881 km and elevation is between 2,266 and 2,749 m), non-lactating female bears are present.</p>

^aAccuracy of the final descriptive statement for lactating and non-lactating female bear distributions was 81.93% and 74.56%, respectively.

Table 2-2. Relative importance of variables from the Genetic Program analysis, calculated as the percentage of model runs ($n = 15$) in which the Genetic Program selected the variable as a predictor in a final best individual (i.e., descriptive statement tree; Fig. 2-4) that was more than 65% accurate.

Variable	Relative Importance	
	Lactating	Non-Lactating
Elevation	28.38%	25.71%
Maximum daily temperature	16.22%	2.86%
Percent cloud cover	14.86%	2.86%
Metabolic rate (kj/d)	10.81%	5.71%
Minimum daily temperature	8.11%	7.14%
Distance to Stream or River	5.41%	2.86%
NLCD	4.05%	8.57%
Distance to forest edge	4.05%	10.00%
Census Home Density	4.05%	5.71%
Percent shade	2.70%	0.00%
Distance to Road or Highway	1.35%	28.57%
NDVI	0.00%	0.00%

Table 2-3. Traditional modeling approaches used to predict species distributions, and their corresponding accuracies for predicting bear presence based on our empirical dataset. All models were fit using the entire suite of variables supplied to the Genetic Program to facilitate direct comparison across methods. Accuracy rates are based on 10-fold cross validation and were calculated for both non-lactating and lactating female bears.

Modeling approach	Accuracy	
	Lactating	Non-lactating
Logistic Regression;	71.18%	63.39%
Linear Discriminant Analysis	64.95%	63.18%
Quadratic Discriminant Analysis	73.55%	58.91%

Literature Cited

- Aanes, R., Saether, B.E. and Oritsland, N.A. (2000) Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography*, **23**, 437 – 443.
- Abu-Hamdeh, N.H. and Reeder, R.C. (2000) Soil thermal conductivity effects of density, moisture, salt concentration, and organic matter. *Soil Science Society of America Journal*, **64**, 1285 – 1290.
- Apps, C.D., McLellan B.N., and Woods, J.G. (2006) Landscape partitioning and spatial inferences of competition between black and grizzly bears. *Ecography*, **29**, 561 – 572.
- Apps, C.D., McLellan, B.N., Woods, J.G., and Proctor, M.F. (2004) Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management*, **68**, 138 – 152.
- Araujo, M.B., and Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527 – 1539.
- Aryal, A., Shrestha, U.B., Ji, W., Ale, S.B., Shrestha, S., Ingty, T., Maraseni, T., Cockfield, G., and Raubenheimer, D. (2016) Predicting the distributions of predator (snow leopard) and prey (blue sheep) under climate change in the Himalaya. *Ecology and Evolution*, **6**, 4065 – 4075.
- Alamgir, A., Mukul, S.A., and Turton, S.M. (2015) Modelling spatial distribution of critically endangered Asian elephant and Hoolock gibbon in Bangladesh forest ecosystems under a changing climate. *Applied Geography*, **60**, 10 – 19.
- Blanchard, B.M. (1983) Field techniques used in the study of grizzly bears. Interagency Grizzly Bear Study Team, Montana State University, Bozeman, Montana.
- Boyce, M.S. and Waller, J.S. (2003) Grizzly bears for the Bitterroot: predicting potential abundance and distribution. *Wildlife Society Bulletin*, **31**, 670 – 683.
- Brown, F.M. (1942) The microscopy of mammalian hair for anthropologists. *Proceedings of the American Philosophical Society*, **85**, 250 – 274.

- Braconnot, P., Harrison, S.P., Kageyama, M., Bartlein, P.J., Masson-Delmotte, V., Abe-Ouchi, A., Otto-bliesner, B., and Zhao, Y. (2012) Evaluation of climate models using palaeoclimatic data. *Nature Climate Change*, **2**, 417 – 424.
- Brown, C.J., O’connor, M.I., Poloczanska, E.S., Schoeman, D.S., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Pandolfi, J.M., Parmesan, C., Richardson, A.J. (2016) Ecological and methodological drivers of species distribution and phenology responses to climate change. *Global Changes Biology*, **22**, 1548–1560.
- Chan, K., Mysterud, A., Oritsland, N.A., Severinsen, T., and Stenseth, N.C. (2005) Continuous and discrete extreme climatic events affecting the dynamics of a high-arctic reindeer population. *Oecologia*, **145**, 556 – 563.
- Colwell R.K., Brehm G., Cardelus C.L., Gilman A.C. and Longino J.T. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**, 258–261.
- Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (2012) COSEWIC Assessment and status report grizzly bear *Ursus arctos* in Canada. COSEWIC, Ottawa, ON, Canada.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J. and Pasteris, P.P. (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, online.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., and Wood, S. (1998) Making mistakes when predicting shifts in species range response to global warming. *Nature*, **391**, 783 – 786.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., and Mace, G.M. (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**, 53 – 58.
- Ferguson, S.H. and McLoughlin, P.D. (2000) Effects of energy availability, seasonality, and geographic range on brown bear life history. *Ecography*, **23**, 193 – 200.
- Fortin, J.K., Schwartz, C.C., Gunther, K.A., Teisberg, J.E., Haroldson, M.A., Evans, M.A., and Robbins, C.T. (2013) Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *Journal of Wildlife Management*, **77**, 270 – 281.

- French, S.P., French, M.G., and Knight, R.R. (1994) Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. *International Conference on Bear Research and Management*, **9**, 389 – 399.
- Fuller, A., Mitchell, D., Maloney, S.K. and Hetem, R.S. (2016) Towards a mechanistic understanding of the responses of large terrestrial mammals to heat and aridity associated with climate change. *Climate Change Responses*, **3**, online.
- Garcia, M.J., Medici, E.P., Naranjo, E.J., Novarino, W., and Leonardo, R.S. (2012) Distribution, habitat, and adaptability of the genus *Tapirus*. *Integrated Zoology*, **7**, 346 – 355.
- Gittleman, J. (1989) Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, NY, USA.
- Gunther, K. (2008) Yellowstone National Park Recreational Use. Page 4 in Schwartz, C.C., Haroldson, M.A. and West, K., editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2007. U.S. Geological Survey, Bozeman, Montana, USA.
- Haroldson, M.A. (2008) Assessing trend and estimating population size from counts of unduplicated females. Page 9 in Schwartz, C.C., Haroldson, M.A. and West, K., editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2007. U.S. Geological Survey, Bozeman, Montana, USA.
- Heller, N.E. and Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14 – 32.
- Helmuth, B., Kingsolver, J.G., and Carrington, E. (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual Reviews in Physiology*, **67**, 177 – 201.
- Huang, S., Chiou, C., Lin, T., Tu, M., Lin, C. and Porter, W.P. (2013) Future advantages in energetics, activity time, and habitats predicted in a high-altitude pit viper with climate warming. *Functional Ecology*, **27**, 446 – 458.
- Hutchinson, G.E. (1957) Concluding remarks, population studies: animal ecology and demography. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415 – 427.

- IPCC (2013): Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex V., and Midgley, P.M. editors. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jenness, R., Erickson, A.W., and Craighear, J.J. (1972) Some comparative aspects of milk from four species of bears. *American Society of Mammologists*, **53**, 34 – 47.
- Jeschke, J.M. and Strayer, D.L. (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences*, **1134**, 1 – 24.
- Jetz, W., Wilcove, D.S., and Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, online.
- Kamath, P.L., Haroldson, M.A., Luikart, G., Paetkau, D., Whitman, C., and Van Manen, F.T. (2015) Multiple estimates of effective population size for monitoring a long-lived vertebrate: an application to Yellowstone grizzly bears. *Molecular Ecology*, **24**, 5507 – 5521.
- Kareiva, P.M., Kingsolver, J.G., and Huey, R.B. (1993) Biotic interactions and global change. United States: online.
- Kearney, M. R. and Porter, W. P. (2004). Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* **85**, 3119–3131.
- Kearney, M. R. and Porter, W. P. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecological Letters*, **12**, 334–350.
- Koza, J.R. (1996) Encyclopedia of computer science and technology, 1996. Genetic programming. Page ___ in Kent, A. and Williams J.G., editors.
- Król, E. and Speakman, J.R. (2003a) Limits to sustained energy intake VI. Energetics of lactation in laboratory mice at thermoneutrality. *Journal of Experimental Biology*, **206**, 4255–4266.
- Król, E. and Speakman, J.R. (2003b) Limits to sustained energy intake VII. Milk energy output in laboratory mice at thermoneutrality. *Journal of Experimental Biology*, **206**, 4267–4281.

- Król, E., Johnson, M.S. and Speakman, J.R. (2003) Limits to sustained energy intake VIII. Resting metabolic rate and organ morphology of laboratory mice lactating at thermoneutrality. *Journal of Experimental Biology*, **206**, 4283–4291.
- Long, R.A., Bowyer, T., Porter, W.P., Mathewson, P., Monteith, K.L., and Kie, J.G. (2014) Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecological Monographs*, **84**, 513 – 532.
- Long, R.A., Bowyer, R.T., Porter, W.P., Mathewson, P., Monteith, K.L., Findholt, S.L., Dick, B.L., and Kie, J.G. (2016) Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape. *Oecologia*, **181**, 709 – 720.
- Martin, J., Basille, M., Van Moorter, B., Kindber, J., Allaine, D., and Swenson, J.E. (2010) Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology*, **88**, 875 – 883.
- Martinez-Minaya, J., Cameletti, M., Conesa, D., and Pennino, M.G. (2018) Species distribution modeling: a statistical review with focus in spatio-temporal issues. *Stochastic Environmental Research and Risk Assessment*, **32**, 3227 – 3244.
- Mathewson, P.D., Moyer-Horner, L., Beever, E.A., Briscoe, N.J., Kearney, M., Yahn, J.M., and Porter, W.P. (2016) Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates. *Global Change Biology*, **23**, 1048 – 1064.
- Mathewson, P.D. and Porter, W.P. (2013) Simulating polar bear energetics during a seasonal fast using a mechanistic model. *PLOS ONE*, **8**, e72863.
- Matthews, E. (1984) Vegetation, land-use and seasonal albedo data sets. Appendix D in Global Change Database, Africa Documentation, NOAA/NGDC.
- McNab, B.K. (2002) The physiological ecology of vertebrates: a view from energetics. Cornell University Press, Ithaca, New York.
- Moe, T.F., Kindber, J., Jansson, I., and Swenson, J.E. (2007) Importance of diel behaviour when studying habitat selection: Examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology*, **85**, 518- 525.
- Moritz, C. and Agudo R. (2013) The future of species under climate change: resilience or decline? *Science*, **341**, 504 – 508.

- Mukul, S.A., Alamgir, M., Sohel, M.S.I., Pert., P.L., Herbohn, J., Turton, S.M., Khan, M.S.I., Munim, S.A., Reza, A.H.M.A., and Laurance, W.F. (2019) Combined effects of climate change and sea-level rise project dramatic habitat loss of the globally endangered Bengal tiger in the Bangladesh Sundarbans. *The Science of the Total Environment*, **663**, 830 – 840.
- Mysterud, A., Stenseth, N.C., Yoccoz, N.G., Langvatn, R. and Steinheim, G. (2001) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature*, **410**, 1096 – 1099.
- Natori, Y., and Porter, W.P. (2007) Model of Japanese serow (*Capricornis crispus*) energetics predicts distribution on Honshu, Japan. *Ecological Applications*, **17**, 1441–1459.
- Nielsen, S., McDermid, G., Stenhouse, G.B. & Boyce, M.S. (2010) Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biological Conservation*, **143**, 1623– 1634.
- Northrup (2012)
- Peck, C.P, van Manen, F.T., Costello, C.M., Haroldson, M.A., Landenburger, L.A., Roberts, L.L., Bjornlie, D.D. and Mace, R.D. (2017) Potential paths for male-mediated gene flow to and from an isolated grizzly bear population. *Ecosphere*, **8**, e01969.
10.1002/ecs2.1969
- Pigeon, K., Cardinal, E., Stenhouse, G.B., and Cote, S.D. (2016) Staying cool in a changing landscape: the influence of maximum daily ambient temperature on grizzly bear habitat selection. *Oecologia*, **181**, online.
- Pimm, S.L. (2008) Biodiversity: climate change or habitat loss – which will kill more species? *Current Biology*, **18**, 117 – 119.
- Porter, W. P., and Gates, D. M. (1969) Thermodynamic equilibria of animals with environment. *Ecological Monographs*, **39**, 227–244.
- Porter, W.P. and Kearney, M. (2009) Size, shape, and the thermal niche of endotherms. *PNAS*, **106**, 19666 – 19672.
- Porter, W. P. and Mitchell, J. W. (2006) Method and system for calculating the spatial-temporal effects of climate and other environmental conditions on animals. U.S. Patent 7,155,377 in December, 2006. <https://www.google.com/patents/US7155377>
- Porter, W.P., Mitchell, J.W., Beckman, W.A., and DeWitt, C.B. (1973) Behavioral implications of mechanistic ecology. *Oecologia*, **13**, 1 – 54.

- Porter, W. P., Munger, J. C., Stewart, W. E., Budaraju, S., and Jaeger, J. (1994) Endotherm energetics: from a scalable individual-based model to ecological applications. *Australian Journal of Zoology*, **42**, 125–162.
- Porter, W. P., Ostrowski, S., and Williams, J. G. (2010) Modeling animal landscapes. *Physiological and Biochemical Zoology*, **83**, 705 – 712.
- Porter, W. P., Sabo, J. L., Tracy, C. R., Reichman, O. J., and Ramankutty, N. (2002) Physiology on a landscape scale: plant– animal interactions. *Integrative and Comparative Biology*, **42**, 431– 453.
- Prentice, A.M., and Prentice, A. (1988) Energy costs of lactation. *Annual Reviews in Nutrition*, **8**, 63 – 79.
- Roberts, D.R., Nielsen, S.E., and Stenhouse, G.B. (2014) Idiosyncratic responses of grizzly bear habitat to climate change based on projected food resource changes. *Ecological Applications*, **24**, 1144 – 1154.
- Savage, V.M., Gillooly, J.F., Woodruff, W.H., West, G.B., Allen, A.P., Enquist, B.J, and Brow, J.H. (2004) The predominance of quarter-power scaling in biology. *Functional Ecology*, **18**, 257 – 282.
- Sawaya, M. A., Ramsey, A. B. and Ramsey, P. W. (2016) American black bear thermoregulation at natural and artificial water sources. *Ursus*, **27**, 129-135.
- Schmidt-Nielsen, K. (1997) Animal physiology: adaptation and environment. Fifth edition. Cambridge University Press, Cambridge, UK.
- Schwartz, C.C., Fortin, J.K., Teisberg, J.E., Haroldson, M.A., Servheen, C., Robbins, C.T., Van Manen, F.T. (2014) Body and diet composition of sympatric black and grizzly bears in the greater Yellowstone ecosystem. *The Journal of Wildlife Management*, **78**, 68 – 78.
- Schwartz, C.C., Haroldson, M.A., White, G.C., Harris, R.B., Cherry, S., Keating, K.A., Moody, D., and Servheen, C. (2006) Temporal, spatial, and environmental influences on the demographics of the Yellowstone grizzly bear. *Wildlife Monographs*, **161**, 1 – 8.
- Sellers, W. D. (1965) Physical climatology. University of Chicago Press, Chicago, Illinois, USA.

- Speakman, J.R. and Król E. (2010a) Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, **79**, 726 – 746.
- Speakman, J.R. and Król, E. (2010b) The heat dissipation limit theory and evolution of life histories in endotherms—time to dispose of the disposable soma theory? *Integrative and Comparative Biology*, **50**, 793–807.
- Speakman, J.R. and McQueenie, J. (1995) Limits to sustained metabolic rate: the link between food intake, basal metabolic rate, and morphology in reproducing mice, *Mus musculus*. *Physiological Zoology*. **69**, 746-769.
- Stockwell D.R.B. and Noble, I.R. (1992) Induction of sets of rules from animal distribution data: a robust and informative method of data analysis. *Mathematics and Computers in Simulation*, **33**, 385 – 390.
- Valvano, J.W., Cochran, J.R., and Diller, K.R. (1985) Thermal conductivity and diffusivity of biomaterials measured with self-heated thermistors. *International Journal of Thermophysics*, **6**, 301 – 311.
- Wickham, J., Homer, C., Vogelmann, J., McKerrow, A., Mueller, R., Herold, N. and Coulston, J. (2014) The multi-resolution land characteristics (MRLC) consortium – 20 years of development and integration of USA national land cover data. *Remote Sensing*, **6**, 7424 – 7441.
- Wilson, A.M. and Jetz, W. (2016) Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. *PLoS Biology*, **14**, online.
- U.S. Fish and Wildlife Service. 1993. Grizzly bear recovery plan. Missoula, Montana, U.S.A., 181 pp. (URL: https://www.fws.gov/mountain-prairie/es/species/mammals/grizzly/Grizzly_bear_recovery_plan.pdf).
- Zhang, Y., Mathewson, P.D., Zhang, Q., Porter, W.P., and Ran, J. (2018) An ecophysiological perspective on likely giant panda habitat responses to climate change. *Global Change Biology*, **24**, 1804 – 1816.

Appendix 1 Parameters for Niche Mapper and their associated sources.

Table A-1. List of parameters for the mechanistic model Niche Mapper, and their associated values and sources.

Parameter	Source	Value
Body mass	Seasonal estimates from Schwartz et al. (2014) ^a	99 – 135 kg
Percent body fat	Seasonal estimates from Schwartz et al. (2014)	13 – 27.5 %
Animal density	Weighted average based on body composition (Schwartz et al. 2014) and density of bone, muscle, fat, and viscera (from Warren Porter)	1033.6 kg/m ³
Basal metabolic rate	Estimate based on standard $\frac{3}{4}$ power function as reported in Savage et al. (2004)	107 W
Pelt reflectivity (350 – 2,500 nm) on the dorsal and ventral surfaces of the head, neck, torso, and legs	Measured from captive bears at Washington State University Bear Research, Ecology, and Conservation Center (WSUBRECC) with field spectrophotometer	Example: torso, dorsal .430, ventral .29
Pelt depth and hair length	Measured from captive bears at WSUBRECC, once in May and once in September. Validated with Brown (1942)	31.4 – 75.9 mm / 52.9 – 82.8 mm
BMR multiplier for lactation	Jenness et al. (1972), Prentice and Prentice (1988), Gittleman (1989)	1.52
Thermal conductivity of flesh	Valvano et al. (1985) and Natori and Porter (2007)	0.4 – 2.8 W/mC
Oxygen extraction efficiency	Schmidt-Nielsen (1997)	25%
Bmr multiplier for activity	Measured from captive bears at WSUBRECC during treadmill trials and doubly labeled water trials. Speed estimates for activity based on IUCN (1974)	1.56

Configuration factors	Warren porter, personal communications	Between animal and sky = 0.5; between animal and ground = 0.3
Soil thermal conductivity	Estimated from Abu Hamdeh and Reeder (2000)	.35 W/mC
Substrate reflectivity	Averaged across multiple vegetation types (Matthews 1984)	26%
Substrate density	Estimated from common rock data available online ^b	2650 kg/m ³
Substrate specific heat	Estimated from common rock data available online ^b	837 J/kg-K
Substrate longwave infrared emissions	Sellers 1965	90%
Animal average height	Measured from captive grizzly bears at WSUBRECC	100 cm
Percent shade	Estimated as percent canopy cover from the National Land Cover Database	WSUBRECC and GRZ 1 – 100%
Cloud cover	Historic weather data available at weatherunderground.com	WSUBRECC 0 – 54.3%; GRZ 0 – 100%
Air Temperature	Recorded at 5 m by a weather station ^c in WSUBRECC and sourced from PRISM Climate Group at Oregon State University	WSUBRECC 1.40 – 33.92 °C; GRZ -10.14 – 29.72 °C

^aSources cited in Appendix A are available in Chapter 2 Literature Cited

^bCommon rock data obtained from: (1) <http://www.engineeringtoolbox.com>; and (2) <http://www.edumine.com/xtoolkit/tables/satables.htm>.

^cWeather station at WSUBRECC located at 46°43'50"N, 117°8'33"W

Appendix 2 Genetic Program parameters

Table A-2. List of evolutionary parameters used to define the Genetic Program algorithm, along with their implementation details and the value for each.

Parameter	Explanation	Value
Population size	The number of individuals evaluated each generation	500
Generations	The number of populations iteratively subjected to a reproduction event	50
Mutation rate (per node)	The probability that a given node within a tree (individual) is subjected to mutation. If a branch node is mutated, it is changed to a new linkage (and, or, and not, or not), each with probability .25. If a leaf node is mutated, it either has its variable reassigned (based on n possible variables in the model, each with probability 1/n), its minimum value adjusted (by a value drawn from a uniform distribution centered at 0 with a range of 40), or its range adjusted (in the same manner as the minimum value), each with a probability of 1/3	0.04
Crossover	The probability that a crossover event occurs between two reproducing individuals	1
Elitism	The probability that the best individual from a previous population asexually reproduces to the next generation (without mutation or crossover)	1
Tournament Size	A sample of the population (taken with replacement) taken to select two parent trees from which to create an individual in the next generation	3