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Behavioral plasticity of large mammals in the Rocky Mountain to variation in temperature

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Abstract Behavioral plasticity, the alteration of behavior in response to stimuli, is becoming increasingly important in the context of rapid climate change. Despite research demonstrating that climatic changes are already impacting species' behavior worldwide, there are relatively few studies that have compared behavioral plasticity in response to increasing temperatures across species. We quantified behavioral plasticity in response to variation in summer temperatures in 17 populations across 9 species of large mammals in the Rocky Mountains. All study populations displayed behavioral plasticity in response to increasing temperatures, modifying their habitat selection and movement characteristics. We also found that there was significant variation in behavioral responses, both within and among populations. Our work demonstrates the capacity (and limits) of large mammals to mitigate rapid environmental change through behavioral plasticity, while simultaneously providing valuable information to wildlife managers on the strategic allocation of limited resources to best facilitate plasticity and population persistence.

Introduction

Climate change is altering temperature dynamics worldwide, resulting in an increase in overall temperatures, more days of extreme heat, and fewer days of extreme cold (Pachauri et al., 2014). In the Rocky Mountains, climatic changes mirror worldwide trends; data suggest an average increase of 2-3°C by 2050 (Halofsky and Peterson, 2018). With increasing temperatures, animals are more susceptible to heat stress which can ultimately lead to mortality. Animals can mitigate this stress by moving to more suitable ranges, adapting, or acclimatizing. Large mammals are often constrained from the first two options. Habitat fragmentation and human development frequently limit the ability of wide-ranging animals to move to more suitable ranges. Large mammals also have a reduced ability to adapt to rapidly changing conditions because their body size and specific life-history traits result in a slower pace over which natural selection can operate (e.g., long generation time, few offspring). To cope with current changing temperature regimes, large mammals must rely primarily on acclimatization, which is most efficiently achieved through behavioral plasticity (Hetem et al., 2014). Behavioral plasticity, or more specifically contextual plasticity, is the alteration of an individual's behavior in response to current exogenous stimuli, experiences, and/or environments (Stamps, 2016). Such plasticity in behavior can have important fitness consequences as it allows individuals to rapidly adjust to exogenous variation such as shifting environmental conditions (Hetem et al., 2014). Despite the rapidly changing climate, behavioral adaptations to extreme heat are poorly understood in large mammals (Fuller et al., 2016). Although research exists regarding the thermoregulatory mechanisms that individual species use to cope with extreme heat, there remains a need for an integrative and comparative analysis of the extent and nature of behavioral plasticity across populations and species (Beever et al., 2017). Here, we examine how 9 species of large mammals change their movement and habitat selection behavior to cope with increasing temperatures.

Our specific research objectives include:

1. Quantify individual behavioral plasticity in response to varying temperatures
2. Quantify the average behavioral plasticity observed in each population
3. Quantify the average variation in behavioral plasticity among individuals within each population.

Methods

Animal location data and study area

We used existing GPS location data from 1068 unique animal-years representing 17 populations of 9 species of large mammals: bighorn sheep *(Ovis canadensis)*, bison *(Bison bison)*, cougar *(Puma concolor)*, elk *(Cervus elaphus)*, moose *(Alces alces)*, mountain goat *(Oreamnos americanus)*, mule deer *(Odocoileus hemionus)*, pronghorn *(Antilocapra americana)*, and gray wolf *(Canis lupus)*. To capture differences in behavioral plasticity among populations of the same species in relation to increasing temperatures, we analyzed multiple populations when possible. This approach also allowed us to measure the behavioral responses of animals that experienced a range of environmental conditions (Table 1). Study populations were primarily distributed throughout western and southern Wyoming (Table 1, Figure 1). In general, the study area was characterized by distinct seasonality, with relatively long cold winters and short, warm summers.

Quantifying individual behavioral plasticity

We operationally defined behavioral plasticity as the degree to which habitat selection and movement characteristics vary across a gradient of temperature. To quantify plasticity at the individual level (Objective 1), we ran a separate resource selection function (RSF) and a simple movement model for each unique animal within a given year from each population during summer (i.e., 15 June to 30 August). RSFs are commonly used to understand the landscape characteristics that are disproportionally used given a domain of availability (Mayor et al., 2009). We used logistic regression models to compare habitat attributes related to thermal regulation (i.e., elevation, aspect, percent canopy cover, and soil moisture) at used points (1) to available points (0) within each individual's summer home range. We then used interaction terms for each of these habitat characteristics with maximum relative daily temperatures across an individual's home range to assess how relative selection for these attributes varied with changing temperatures. In addition, we quantified individual movement speed and used a generalized linear model to test how individual speed varied across days of varying temperatures in the summer. All explanatory variables were scaled and centered, allowing for direct intra- and inter-population comparisons.

Calculating behavioral plasticity among and within populations

To quantify and compare mean population behavioral plasticity across populations (Objective 2), we calculated a plasticity metric from the individual-level models for each population. This metric represents the average beta-coefficient (i.e., the strength of selection) from each interaction term between each habitat covariate and temperature in the RSFs and the movement model. The metric was calculated by taking a weighted mean of the absolute value of these individual beta-coefficients using the inverse of the SE as the weight (Stamps, 2016). For example, in the Seminoe population of bighorn sheep, there were 34 individual animal-years, so the population plasticity metric represents the weighted mean of 34 individual beta-coefficients for each habitat variable (n=4) and

Species	Population	$n_{population}$	Dates	Fix rate (hrs)
Bighorn Sheep	1. Seminoe	34	2010-2012	5
	2. Jackson	5	2010-2012	2.5
	3. N Range	11	2017-2019	2
Bison	4. Interior	124	2004-2018	2
	5. N Range	157	2007-2018	2
Cougar	6. N Range	14	2016-2019	0.5
Elk	7. Sierra Madre	88	2012-2018	1.5
	8. White Mountain	55	2010-2014	3
Moose	9. Jackson	66	2005-2009	1
	10. Sublette	132	2011-2014	1
Mountain goat	11. Palisades	26	2012-2016	5
Mule deer	12. Choke Cherry	102	2011-2018	2
	13. Hoback	91	2014-2019	2
Pronghorn	14. Shirley Basin	63	2018-2019	2
	15. Sublette	40	2010-2017	2
Wolf	16. Interior	10	2005-2019	0.5
	17. N Range	50	2001-2019	0.5

Table 1. Metadata of 17 study populations (9 species) of large mammals in western Wyoming (USA) 2001-2019. Numbers in population column correspond with those in Figure 1.

movement speed (n=1).

To quantify and compare mean variation in plasticity among individuals within each population (Objective 3), we determined, for each population, a single population-level metric of individual variation. To calculate this metric, we took the square root of the weighted variance of all beta-coefficients within a population.

Preliminary results

Individual behavioral plasticity

The majority of individuals displayed behavioral plasticity to increasing temperatures, as a mean of 80% (SD = 0.167) of individuals across populations had at least one significant ($P < 0.05$) beta-coefficient. The Northern Range populations of bighorn sheep and cougar had the highest proportion of individuals with at least one significant beta-coefficient (proportion = 1.0), while the Seminoe population of bighorn sheep had the lowest (proportion = 0.32) (Figure 2).

Behavioral plasticity among and within populations

We found that all populations displayed behavioral plasticity by modifying their habitat selection and movement characteristics as temperatures increased, although the overall magnitude varied (Figure 3). Pronghorn displayed the highest degree of mean population plasticity, ranking both first (Sublette population) and second (Shirley Basin population) in the comparative analysis, while the Northern Range population of cougar displayed the lowest degree of mean population plasticity. In the species with multiple populations, there was a similar degree of mean population behavioral plasticity displayed across populations. For example, both populations of bison displayed a low amount of mean population plasticity to

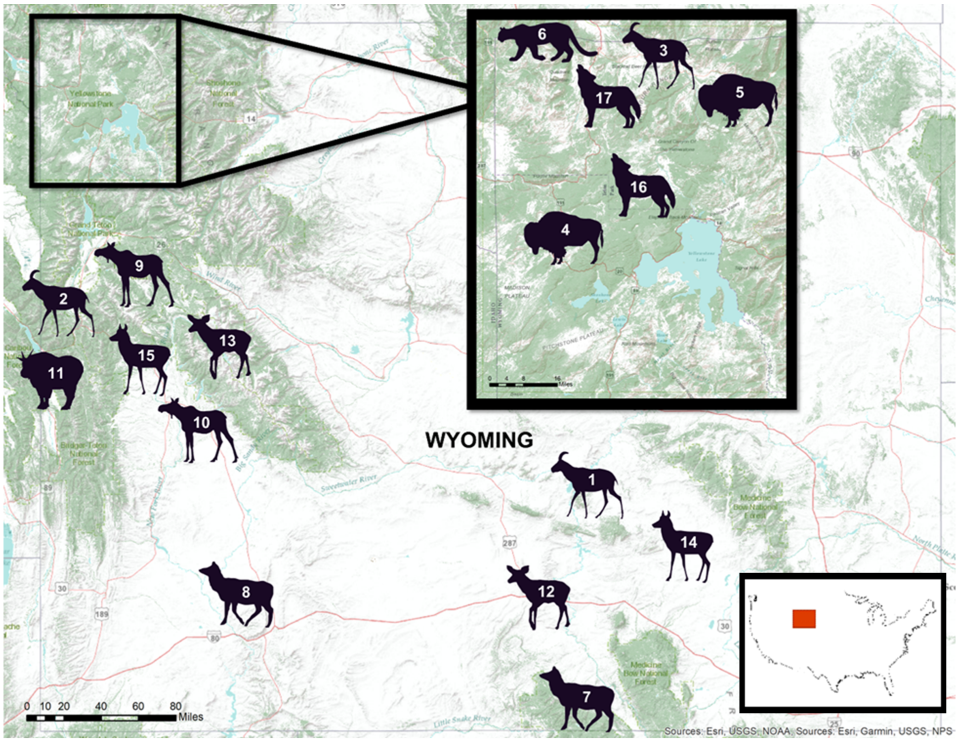

Figure 1. Map of 17 study populations (9 species) of large mammals in western Wyoming (USA) 2001-2019 – 1) Rocky Mountain bighorn sheep: Seminoe population, 2) Rocky Mountain bighorn sheep: Jackson population, 3) Rocky Mountain bighorn sheep: Jackson population, 4) American bison: Interior population, 5) American bison: Northern Range population, 6) cougar: Northern Range population, 7) Rocky Mountain elk: Sierra Madre population, 8) Rocky Mountain elk: White Mountain, 9) Shiras moose: Jackson population, 10) Shiras moose: Sublette population, 11) mountain goat: Palisades population, 12) Rocky Mountain mule deer: Choke Cherry population, 13) Rocky Mountain mule deer: Hoback population, 14) American pronghorn: Shirley Basin population, 15) American pronghorn: Jackson population, 16) gray wolf: Interior population, and 17) gray wolf: Northern Range population. Detailed metadata for each population is available in Table 1.

temperature, while both populations of mule deer displayed a moderate amount.

The specific behavioral responses to increasing temperatures varied across populations. On average, as temperatures increased, 10 of 17 populations selected areas that had relatively higher elevations, 11 of 17 populations selected areas with more northeasterly aspects, 7 of 17 populations selected areas with relative higher percentages of cover, 14 of 17 populations selected areas with a higher potential for wetness, and 8 of 17 moved at relatively lower speeds (Figure 4).

Overall, mean variation in behavioral plasticity among individuals within each population was relatively high. Within a population, there were often some individuals that responded strongly in one direction (e.g., moved up in elevation), while others responded in the opposite direction (e.g., moved down in elevation). However, mean variation in plasticity among individuals within each population was relatively consistent across populations, with the exception of the Shirley Basin pronghorn and White Mountain elk, which displayed considerably higher among-individual variation in plasticity than the others (Figure 5).

Conclusions

Behavioral plasticity can act as the 'first line of defense' for species to cope with rapid change. Large mammals in the Rocky Mountains appear to have

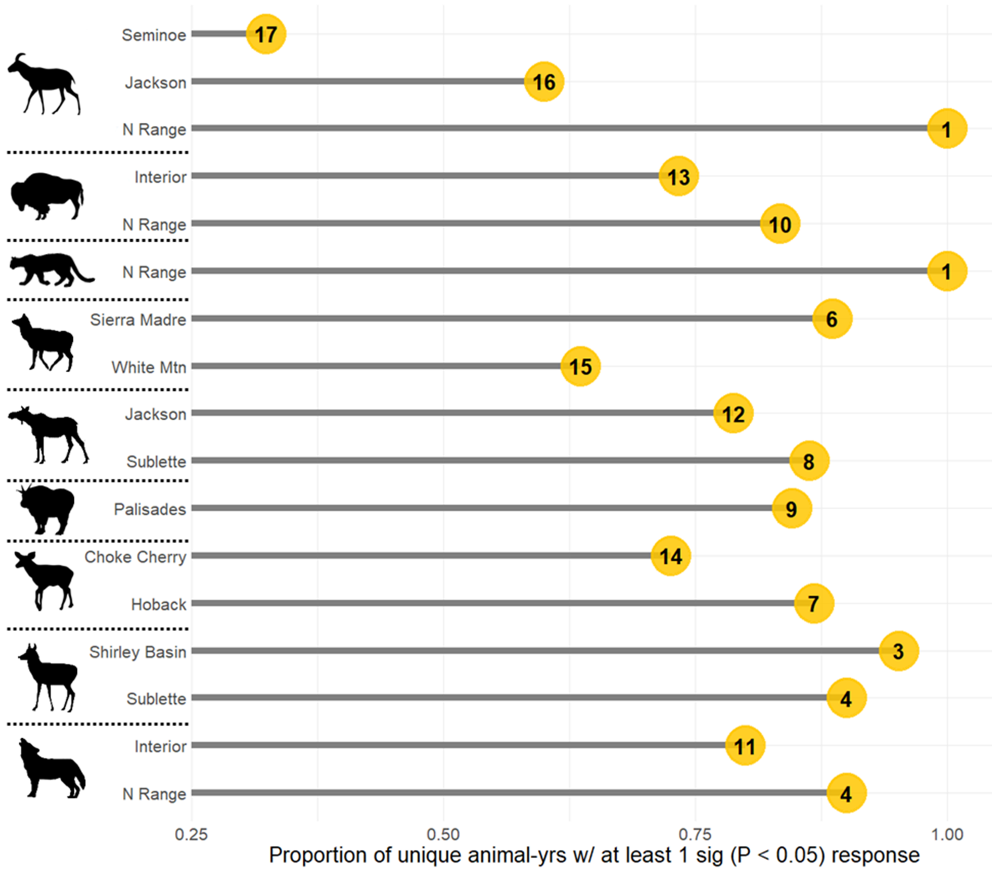

Figure 2. Proportion of unique individual animal years that displayed behavioral plasticity to changing temperatures (i.e., had at least one significant ($P < 0.05$) beta-coefficient). Numbers in circles indicate the rankings of individual behavioral plasticity from highest (1) to lowest (17).

substantial behavioral plasticity in response to variation in thermal conditions during summer, providing them with a critical tool for acclimatizing to rapidly changing, and potentially stressful, temperatures. Further, the specific behaviors individuals used varied widely, suggesting that there are many effective strategies to behaviorally mitigate heat stress. Behavioral plasticity may have different net benefits and costs for different individuals (e.g., males vs. females), and that variation among individuals may provide some type of portfolio effect within populations to better protect them against an increasing risk of heat stress (Schindler et al., 2010). Our results describe the plethora of behaviors large mammals are employing to mitigate the negative ramifications of climate change and collectively provide novel insight into the factors that may facilitate or constrain the evolution of plasticity.

In addition to the ecological contribution, our research may also provide managers with information regarding species' preferred "strategies" and overall behavioral-plasticity capacity. This knowledge can assist in making ecologically-informed management decisions to ensure viable wildlife populations persist in a rapidly changing climate (Beever et al., 2017). Furthermore, our results demonstrate that the magnitude and preferred "strategy" of behavioral plasticity is not homogeneous within a population or species (e.g., some individuals seek tree cover as temperatures increase, while others move to areas with a greater potential for wetness/moisture). To give populations the best chance of persistence in the face of climate change, managers may protect a diversity of environmental features that facilitate different pathways for behavioral plasticity at an individual level. Finally, our comparative approach offers insight

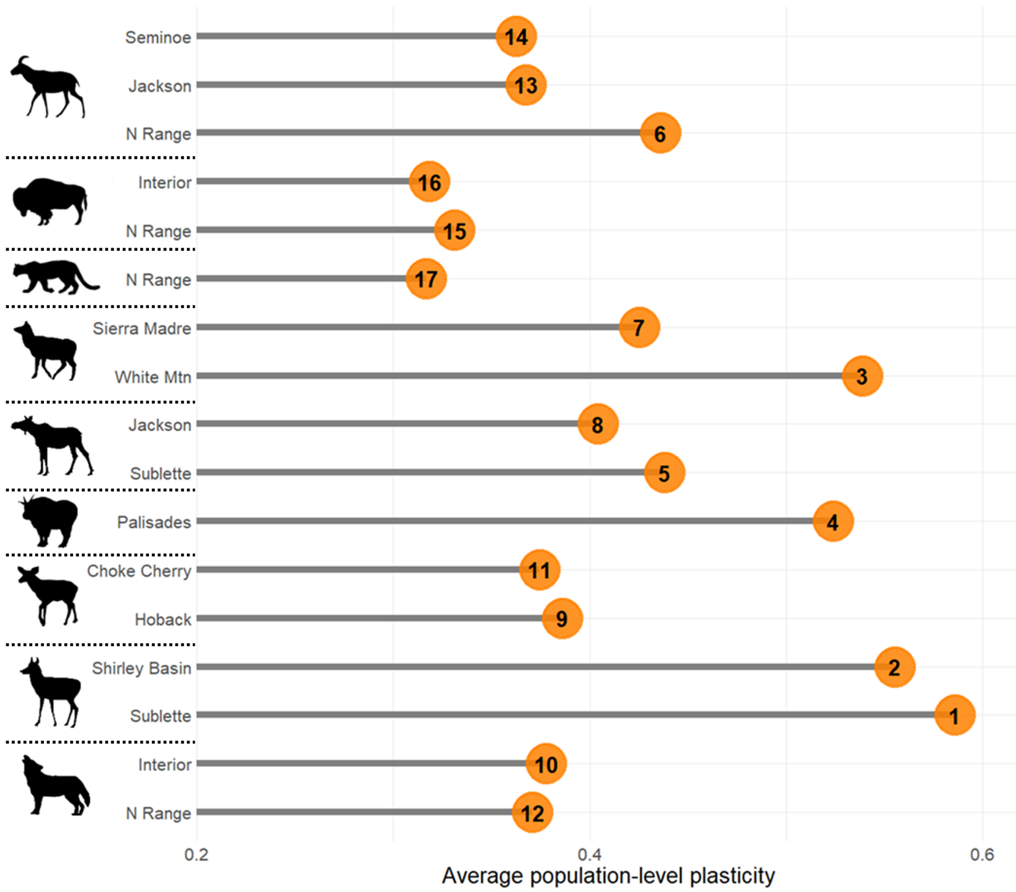

Figure 3. Mean population behavioral plasticity in selection for physical resources and movement speed in response to increasing temperatures. Numbers in circles indicate the rankings of mean population behavioral plasticity from highest (1) to lowest (17).

into which populations and species may demonstrate more or less behavioral plasticity in response to increasing temperatures, which is an important component of species' adaptive capability. This information could help managers tasked with conserving multiple populations and species to prioritize where to allocate limited resources.

Future work

In addition to the results presented here, we also tested hypotheses to explain the observed variation and examine the importance of environmental context and endogenous constraints on the expression of behavioral plasticity in response to rapidly changing conditions. Together, this work constitutes Rebecca R. Thomas-Kuzilik's master's thesis, which was accepted at the University of Wyoming in fall 2021. It will be published as a peer-reviewed article – ideally in the form of a monograph – in the near future.

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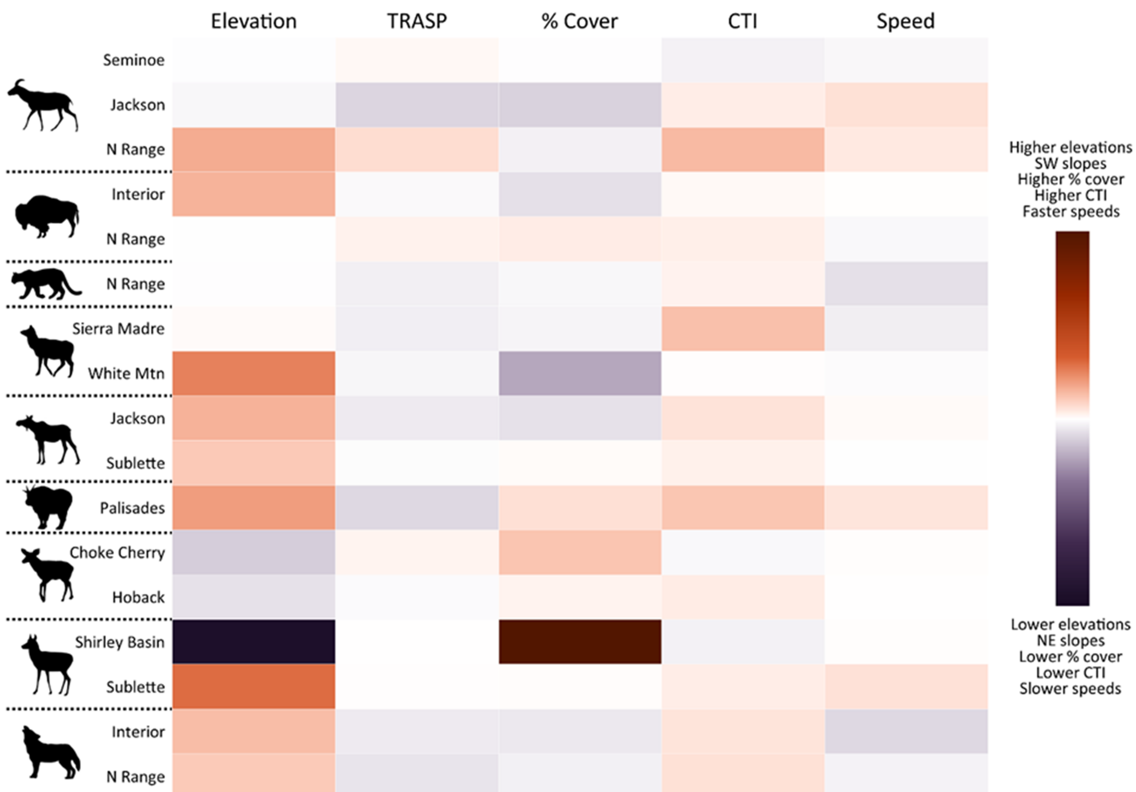

Figure 4. Mean relative selection for physical resources and changes in movement speed in response to increasing temperatures. Purple boxes indicate a negative behavioral plasticity beta coefficient, red indicates a positive behavioral plasticity beta coefficient. The intensity of color indicates the relative magnitude of behavioral plasticity displayed by each population, with darker colors representing a greater change in behavior as temperatures increased. For example, the Shirley Basin population of pronghorn moved to relatively lower elevations and areas with relatively higher percent tree cover as temperatures increased. TRASP: topographic radiation aspect index; CTI: compound topographic index.

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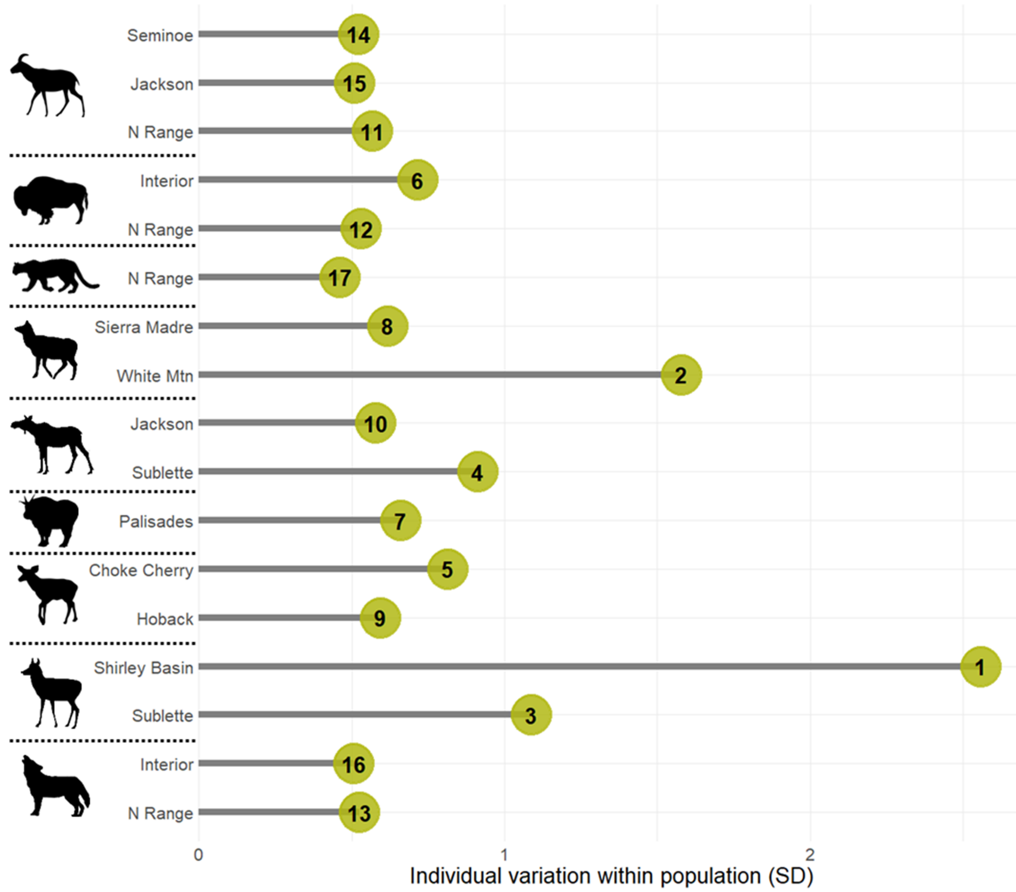

Figure 5. Mean variation in behavioral plasticity among individuals within populations in the selection for physical resources and movement speed in response to increasing temperatures. Numbers in circles indicate rankings of mean variation in behavioral plasticity from highest (1) to lowest (17).

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