

Lay Summary

Climate change could benefit marmot populations as longer summers offer more time to look out for predators and gain mass for the next hibernation. Rising temperatures with global warming may also lead to marmot population growth if the resulting increased pup summer survival (from increased awareness of predators) outweighs the potential decrease in pup winter survival (from decreased food intake).

Does current weather or seasonality influence antipredator vigilance in a hibernating mammal?

Karsten Bobb^a, Katie A. Adler^{a,b}, Julien G.A. Martin^{a,c}, and Daniel T. Blumstein^{a,b}

^aRocky Mountain Biological Laboratory, Box 519, Crested Butte, CO 81224, USA, ^bDepartment of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA, ^cDepartment of Biology, University of Ottawa, Ottawa, Ontario, K1N 6N5, Canada

Address correspondence to D.T. Blumstein. E-mail: marmots@ucla.edu

As the global climate changes, temperatures are rising, snow is melting earlier, and rainfall is becoming more variable. These climatic changes create an ecological mismatch as animals find themselves maladapted to these different environmental conditions. While prior work has shown how animals respond to these changes physiologically and behaviorally, few have specifically investigated antipredator behavior, which is an essential activity for most species. In many

species, such as the behaviorally plastic yellow-bellied marmot (*Marmota flaviventer*), there are direct fitness tradeoffs between allocating time and energy to antipredator vigilance and foraging. To discover how these tradeoffs are affected by climate change, we studied how temperature, snowmelt date, and July rainfall affected the proportion of time marmots allocated to vigilance and foraging during bouts of foraging. While rainfall explained no significant variation in time allocated to vigilance or foraging, other aspects of both seasonality and weather had significant impacts on this time allocation. As snow melted earlier, marmots spent a greater proportion of time being vigilant (though foraging was not significantly impacted). Longer active seasons that come with early snowmelt are associated with increased juvenile survival and marmot population growth. As snow melts earlier with climate change, individuals may exhibit heightened vigilance and have more time to gain mass, which increase summer and winter survival, respectively. Therefore, these improved fitness attributes may result in an increase in marmot population numbers. As temperatures increased, juvenile marmots became relatively more vigilant and allocated less time to foraging compared to adults. This is likely to increase juvenile summer survival and decrease juvenile winter survival (unless the longer active season allows them to overcome shortened foraging times). Juvenile survival rate is one of the major drivers of marmot population growth, so these trends could have powerful impacts at the population level. Further research is necessary to determine whether these findings extend to related species.

Key words: climate change, thermoregulation, thermal plasticity, antipredator behavior, yellow-bellied marmots

INTRODUCTION

Recent reports on climate change present evidence of increasing global temperatures, especially terrestrial air temperatures, and increased frequency and intensity of natural disasters, such as heatwaves and droughts (Calvin et al., 2023; Intergovernmental Panel on Climate Change 2023). Alpine and arctic ecosystems have been identified as particularly vulnerable to this warming (Intergovernmental Panel on Climate Change 2023). These climatic changes create an ecological mismatch as the environmental conditions that shaped the evolution of current animal physiology and behavior are no longer present (Fuller et al. 2010; Huey et al. 2012). Many studies have investigated how climate change has impacted animal physiology and behavior in general, particularly how individual plasticity may aid organisms in adapting to environmental change, but antipredator behavior has been relatively less studied (Beever et al. 2017; Buchholz et al. 2019; Cockrem 2022). Antipredator behavior merits additional study as it has direct links to survival and, by extension, fitness. Therefore, we examine how temperature, rainfall, and snowmelt timing, all factors changing in a warming environment, affect vigilance while foraging in a hibernating rodent.

With an emphasis on a warming climate, numerous studies have explored how higher temperatures have impacted animal thermoregulation and activity levels, which then mediate animal behavior (Cooper et al. 2019; Funghi et al. 2019; Mella et al. 2024). For ectotherms, which cannot regulate their body temperatures independently and thus rely on their environment for heating, several studies have found that elevated ambient temperatures increase activity levels, which is associated with increased aggressiveness and boldness (Biro et al. 2010; Pruitt et al. 2011). On the other hand, recent research on endotherms, which thermoregulate primarily through controlling their metabolic heat production, has primarily examined the effects of heat

stress on both physiological and behavioral thermoregulation (Boyles et al. 2011; Cooper et al. 2019; Hetem et al. 2019; Mella et al. 2024).

Heat stress is of concern for endotherms because their metabolic processes naturally produce heat, so their energy expenditure is limited by how much heat they can dispel (heat dissipation theory; Rogers et al., 2021). For instance, koalas (*Phascolarctos cinereus*) lowered their body temperature in the morning of a particularly hot day as if in preparation for the heat (Mella et al. 2024). Zebra finches (*Taeniopygia guttata*) and cheetahs (*Acinonyx jubatus*) adjusted foraging and hunting times respectively during heat waves with cheetahs becoming more crepuscular and zebra finches foraging more in the cooler morning hours when afternoon temperatures were anticipated to be extremely high (Funghi et al. 2019; Hetem et al. 2019).

Such behavioral shifts can have significant impacts on individual fitness, population dynamics, and species survival. In species where individuals have thermal behavioral plasticity, as temperatures increase, some individuals may become relatively less bold or their behavioral response may become less predictable overall (Biro et al. 2013; Briffa et al. 2013; Moss and While 2021). This is important because increased boldness is associated with both higher growth and mortality rates since bold individuals more often risk foraging when predators are present (Stamps 2007). These few examples demonstrate the complexity of climate change's ecological impacts on survival, which has important demographic consequences.

The time and energy an organism has to complete various tasks both daily and over its lifetime are finite (Perrin and Sibly 1993; Pollard and Blumstein 2008; Dunbar et al. 2009). Therefore, the more time and/or energy an organism devotes to one activity, the less it has for another. Temperature can alter these temporal and energetic tradeoffs, either directly through increased time and energy devoted to thermoregulatory behaviors like seeking shade or escaping to burrows (thermal refugia), panting or licking (evaporative heat loss), and splooting, tree-

hugging, or other forms of expelling heat through conduction (Buchholz et al. 2019) or indirectly by altering other processes like metabolic rate (Biro et al. 2010) and cognitive function (Soravia et al. 2023). Typically, more time and energy is allocated to the activity with the greatest fitness consequences (Perrin and Sibly 1993), but for some organisms, competing activities have relatively equal weight in terms of survival and/or reproduction. For example, yellow-bellied marmots (*Marmota flaviventer*) must balance allocating time and energy to foraging to gain enough mass to survive winter hibernation while also allocating time and energy to vigilance to avoid predation and ensure summer survival (Blumstein et al. 2006). For this reason, yellow-bellied marmots are an ideal species to study ecological tradeoffs, particularly in the face of climate change.

The study of temperature effects on antipredator behavior is especially important because of these tradeoffs and the direct fitness outcomes of antipredator behavior modifications. Changes in antipredator behavior immediately impact organism survival rates by altering their vulnerability to predation. This may have implications for predator-prey dynamics and species survival. However, these impacts are often nuanced because behaviors that reduce the likelihood that an organism is attacked may increase its chances of capture and vice versa (Lind and Cresswell 2005). This is related to the great diversity of behavioral defenses used by prey from avoidance strategies, such as camouflage or shifts in daily activity to times when predators are less active, to evasion tactics of freeze, flight, or fight (which could include alarm calling, physical attacks, multiple lure displays, and much more) (Curio 2012), all of which have varying efficiencies and costs, resulting in variable impacts on fitness. Additionally, organisms with favorable adaptations for predator avoidance and/or evasion may have lower reproductive success and therefore lower or comparable fitness to their conspecifics with lower survival rates but higher reproductive rates (Ives and Dobson 1987 Sep 1; Lind and Cresswell 2005). For

instance, an individual with higher body mass may have higher prey vulnerability but also the capacity to produce and rear more offspring. Essentially, antipredator behavior's connection to fitness is complicated due to frequently conflicting effects on survival and reproductive success.

Existing research on how temperature affects antipredator behavior has focused extensively on ectotherms. Results vary by species and individuals and often illustrate the presence of individual thermal plasticity (Biro et al., 2010; Briffa et al., 2013; Gomes et al., 2002; Mori & Burghardt, 2004). Some ectotherms, like Sousa's snouted tree frogs (*Scinax hiemalis*), guppies (*Poecilia reticulata*), and some species of snakes (such as *Coluber constrictor*, *Natrix maura*, and *Sistrurus catenatus*) are more active, aggressive, and/or have more sensitive antipredator responses at higher temperatures while others, including damselfish (*Pomacentrus chrysurus*) under restricted food availability and other species of snakes (such as *Thamnophis radix*) responded more passively or not at all to predatory stimuli at higher temperatures compared to lower temperatures (Gomes et al., 2002; Lienart et al., 2014; Mori & Burghardt, 2004; Weetman et al., 1998).

Only a few studies have investigated temperature effects on antipredator behavior for endotherms, and those were primarily focused on birds. One such study found that in addition to heat impacting animal behavior through metabolic rate changes, elevated temperatures impair cognition, which can significantly hinder an animal's antipredator behavior (Soravia et al. 2023). Not only does heat stress impact an animal in the present, but it can also have long term effects. For example, southern pied babblers (*Turdoides bicolor*) that experienced heat stress during rearing were shown to have diminished learning performance and foraging and reproductive success as adults (Soravia 2022; Soravia et al. 2024). We know comparatively less about mammals' antipredator responses to heat.

Yellow-bellied marmots are hibernating, ground-dwelling, sciurid rodents and are an ideal species to start filling this knowledge gap because these marmots experience a direct tradeoff between allocating time to vigilance (to survive the summer) and foraging (to gain enough mass to survive winter hibernation) (Blumstein et al. 2006). Furthermore, we study marmots in the upper Colorado River Basin, which has suffered from increasingly severe heatwaves and drought due to decreased snowpack, increased winter melt, and falling stream flows, all of which are compounded by rising air temperatures, making it an appropriate location to study the effects of climate change on antipredator behavior (McCoy et al. 2022; Bolinger et al. 2023). Existing research has shown that marmots avoid being active during extreme temperatures (too hot or too cold), but if forced by energy requirements to forage in unfavorable thermal conditions, they tend to engage in short bouts of foraging with breaks to cool off on rocks in the wind (Melcher et al. 1990). Interestingly, marmots sometimes foraged in extreme temperatures when they had not used all available opportunities to forage in moderate temperatures at another point in the day (Melcher et al. 1990). This could be due to foraging limitations imposed by time required for digestion, which has been found to restrict foraging behavior in some small homeotherms (Weiner 1992). Marmots have large caecums that necessitate periods of fermentation digestion between bouts of foraging (Armitage 2014). This added digestion constraint makes marmots particularly interesting to study. Herbivores, including marmots, experience additional thermoregulatory challenges in high temperatures because the detoxification of consumed plant secondary metabolites hinders thermoregulation, making heat stress of increased concern for these animals (Beale et al. 2018).

Much is known about marmot antipredator behavior that permits us to develop focused hypotheses. For instance, several prey-specific factors influence vigilance, including group, environmental, and internal state conditions (Chmura et al. 2016). Socially, marmots foraging in

smaller groups (Carey and Moore 1986; Beauchamp et al. 2021), with juveniles present, and on the outside of the group (Di Blanco and Hirsch 2006) are typically more vigilant. Alarm calls by conspecifics, especially juveniles, elicit increased vigilance in fellow marmots (Blumstein and Daniel 2004; Blumstein et al. 2008). Environmentally, marmots are less vigilant on steep slopes (Blumstein et al. 2004) and more vigilant when their view is obstructed (Bednekoff and Blumstein 2009). Animals farther from safety (i.e., burrows) are also more vigilant (Carey and Moore 1986; Stankowich and Blumstein 2005; Mateo 2007). Marmots in areas of higher human activity spend more time being vigilant than foraging but become less sensitive to human approach over time (Uchida and Blumstein 2021). Finally, individual factors, such as personality, with increased boldness leading to less vigilance and greater risk-taking (Dammhahn and Almeling 2012); age, with juveniles being less vigilant, perhaps due to higher energy requirements (Carey and Moore 1986; Bachman 1993; Arenz and Leger 2000; Bednekoff and Blumstein 2009); sex, with males being more responsive to alarm calls (Lea and Blumstein 2011a) and female vigilance being more impacted by social group size (Mady and Blumstein 2017); body condition, with faster, healthier marmots being more responsive to predators (Blumstein et al. 2004; Lea and Blumstein 2011b); stress levels (Mateo 2007); and illness, with infections corresponding to decreased antipredator response (Crane et al. 2011); impact animal vigilance (Chmura et al. 2016). These factors provide insights into how climatic characteristics may impact vigilance while exposing a need for additional study of climate effects on animal vigilance.

To study the potential impacts of temperature, rainfall, and length of growing season on marmot vigilance, we quantified the percentage of time allocated to foraging versus vigilance in systematically collected two-minute foraging focal observations (hereafter known as “focal”) while animals were foraging. We noted the temperature when the focal was conducted, the date

of snowmelt for the marmot's colony, and the amount of rain in a key month (July). We predicted the following.

First, if marmots forage for shorter intervals of time during extreme temperatures (Melcher et al. 1990), and energy requirements remain constant (or increase), we predict marmots will allocate a greater proportion of this time to foraging and less to vigilance as temperatures rise.

Second, if early snowmelt corresponds to a longer growing season and increased food availability (Van Vuren & Armitage, 1991), we anticipate marmots will be more vigilant when snow melts early as seasonal food intake requirements (to achieve sufficient mass for winter survival by the end of the summer) will be spread out over more days. This may reduce their daily energy requirements and allow for less time allocation to foraging and more to vigilance.

Finally, marmot growth rates decrease in drought conditions, particularly for juveniles (Lenihan and Van Vuren 1996; Armitage 2013). This is likely due to an increased resting metabolic rate that marmots experience during droughts (Armitage 2014). If marmots must allocate more time to foraging to meet the higher energy requirements that come with an elevated metabolic rate, we hypothesize that less time will be allocated to vigilance as rainfall decreases.

METHODS

Model species and field site

Yellow-bellied marmots are large, social, semi-fossorial ground squirrels and generalist herbivores that live primarily at high elevation in the Northwestern U.S. (Feldhamer et al. 2003). They are prey to several species, principally: coyotes (*Canis latrans*), badgers (*Taxidea taxus*), American martens (*Martes americana*), black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*), mountain lions (*Felis concolor*), wolves (*Canis lupus*), and raptors like red-tailed hawks (*Buteo jamaicensis*), and golden eagles (*Aquila chrysaetos*) (Van Vuren 1991; Van Vuren 2001; Armitage 2004). We studied marmots in and around the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA (38°57'N, 106°59'W).

Trapping and identifying

Marmots at each colony were trapped using Tomahawk wire traps baited with horse feed mixed with peanut butter. During processing, each marmot was tagged with a metal size 3 self-piercing strap tag on each ear and given a mark on their back using Nyanzol A fur dye (Armitage 1962). This ensured certain identification of marmots by ear tags when trapped and allowed for identification of marmots by fur mark at a distance (20-150m) during observations.

Quantifying vigilance: foraging focals

During regular observations (0700-1100 h and 1600-1900 h) we identified a focal foraging individual and, for two minutes, scored behavioral transitions using an established ethogram (Table 1). In addition to the marmot's identity, we noted the time; date; colony; number of other marmots within a 10-meter radius; the slope, angle, substrate (dirt, stones, talus, low vegetation, or high vegetation) where the marmot foraged; and distance from the marmot to the nearest

burrow. Focals were dictated into voice recorders and scored using JWatcher 1.0 (Blumstein & Daniel 2000). Using JWatcher, we calculated the proportion of time in sight that the focal marmot allocated to foraging and looking (behavior quantified for vigilance).

Environmental data collection

Hourly temperatures in the upper East River Valley (where the marmot colonies are located) were collected from the Gothic Research Meadow weather station (38.96, -106.99) for each hour that a focal was recorded. The time each focal was taken was rounded to the nearest hour to synchronize the focal time with the time of the closest temperature recording (Gothic Weather 2024). Focals were recorded within 2.5 km of the weather station, so the temperature recordings are somewhat relative rather than absolute.

We created polygons around marmot colonies and, using the RMBL Spatial Data Platform (Rocky Mountain Biological Laboratory 2002), measured the date for each colony in a given year at which snow was no longer detected via remote sensing at $\leq 3\text{cm}$ resolution. This allowed us to quantify the start of the growing season for plants and active season for marmots.

We chose to analyze daily average rainfall for solely the month of July because monsoon season begins in July. Thus, July is a key month for precipitation because by then the soil moisture from winter snow has dissipated, leaving plants to depend on rainfall for additional growth and maintenance (Comstock and Ehleringer 1992). Therefore, changes in rainfall on productivity would be most clearly observed during this month. Daily rainfall for July was collected from a private weather station (maintained by billy barr) adjacent to the Gothic townsite (38.962914890, -106.992764274) (barr 2002).

Statistical analyses

Before analysis, we recategorized substrate to combine low vegetation (LV) and dirt (D) since both surfaces are easily maneuverable and afford good visibility while talus (T) and stones (S) were combined because these substrates are similar in their difficult maneuverability. High vegetation (HV) remained its own category as it provides poor visibility and difficult maneuverability. Following Chmura et al. (2016), only focals lasting 60 seconds or longer were included in the analysis to exclude observations where marmots were out of sight for the majority of the focal.

To evaluate temperature and snowmelt date effects on time allocated to vigilance while foraging, we fitted a linear mixed effects model to explain variation in the proportion of time allocated to vigilance (we combined both stand look and rear look) during the bout of foraging. We fitted the following fixed effects: temperature, date of snowmelt, valley position (up valley or down valley), day of year, time that focal was collected, the number of marmots within 10 m, substrate (high vegetation, low vegetation, stones and talus), age class (juvenile, yearling, adult), and sex. We included marmot identity (unique ID), year, and colony as random effects. We fitted a second model to explain variation in the proportion of time allocated to foraging (with the same fixed and random effects as the first model). In both models, all continuous variables were scaled in R (Version 4.3.2; R Core Team 2024) using the ‘scale’ function. Effect sizes were calculated using the ‘partR2’ function (Version 0.9.2; Stoffel et. al, 204), which yielded marginal and conditional r-squared values for each variable fitted to the model. Our full data set used for these analyses contained a total of 1607 observations from 369 individuals (176 males, 193 females; X adults, X yearlings, and X juveniles) studied across 18 years.

For our final question, we analyzed July precipitation in two ways: by calculating average daily rainfall and the proportion of July days with rainfall. Each of these were used as independent variables in separate mixed effects models. We fitted the same two mixed effects

models (one for vigilance and another for foraging) as the first two questions for these two rainfall measures using the new July-limited data set, including average daily rainfall or proportion of days with rainfall instead of temperature and snowmelt date. For the foraging and July average daily precipitation model, year was omitted as a random effect to remove singularities since year explained no variance in this model. Our substantially smaller data set contained 251 observations of 154 individuals (66 males, 88 females; X adults, X yearlings, and X juveniles) across 15 years.

In a post hoc analysis, we explored the effect of distance to burrow as a fixed effect for the foraging and average daily rainfall models. We predicted that marmots may feel safer closer to their burrows where they can make a quick escape and could be less vigilant as a result (safer places hypothesis; Monclús et al. 2015). Formally, we tested this by adding burrow distance as a main effect and as an interaction with average daily rainfall. To do so, we categorized the numerical distances as “low” (at or below the median distance of three meters) or “high” (above the median distance of three meters). To avoid losing many observations and because distance to burrow is often not recorded when the burrow is far away, we recategorized NAs as “high.” Distance to burrow did not explain any significant variation as a fixed effect nor as an interaction with average daily rainfall, so after this exploration, we left it out of the final analyses.

In addition to these main effect analyses, we examined interactions between age class and our fixed effects of interest (snowmelt date, temperature, July average daily rainfall, and proportion of July days with rainfall) and between sex and these fixed effects. This allowed us to analyze whether the varying energy requirements of different age groups and sexes influenced the relationship between our fixed effects and dependent variables (vigilance and foraging). Only the significant interactions were kept in the models. We checked distributional assumptions for our

models using the package ‘performance’ (Version 0.12.0; Lüdecke et. al, 2021) and ‘DHARMA’ (Version 0.4.6). For all models, the variance inflation factors were below three, residuals were relatively normal, and the q-q plots were straight.

All statistical analyses and modeling were conducted using the R programming environment (Version 4.3.2; R Core Team 2024). We used the packages ‘lme4’ (Version 1.1-35.4; Bates et. al, 2015) and ‘lmerTest’ (Version 3.1-3; Kuznetsova et. al, 2017) to build models, ‘sjPlot’ (Version 2.8.16; Lüdecke et. al, 2024) and ‘patchwork’ (Version 1.2.0) to visualize the data, ‘MuMIn’ (Version 1.48.4; Bartón et. al, 2024) to determine the range of the data, and ‘partR2’ (Version 0.9.2; Stoffel et. al, 2024) to calculate effect sizes for each fixed effect.

RESULTS

Using the full data set, snowmelt date ranged from 17 April to 19 June, and temperature ranged from -0.1 °C to 23.4 °C. Snowmelt date explained significant variation on yellow-bellied marmot vigilance while foraging (Table 2). Earlier snowmelt dates were associated with decreased marmot vigilance while foraging (estimate = -0.002, $P = 0.037$; Fig. 2). However, the effect size was very small (partial- $r_m < 0.0001$, partial- $r_c = 0.208$; Table 2). While temperature did not have a significant effect on time allocated to vigilance as a main effect (estimate = -0.008, $P = 0.281$; Table 2), the interaction between age class and temperature was significant in explaining variation in vigilance as juveniles allocated more time to foraging relative to adults as temperatures increased (estimate = 0.033, $P = 0.017$; Table 2). Neither the average daily rainfall (estimate = -0.013, $P = 0.329$; Table 3) nor the proportion of days with rainfall (estimate = -0.003, $P = 0.821$; Table 4) had a significant effect on marmot vigilance. Some of the fixed effects included in the models had significant impacts on marmot vigilance, which was consistent with prior studies. Across all three vigilance models, the number of marmots within 10 meters had a

significant effect on marmot vigilance (though the degree of significance varied slightly from model to model). Marmots were less vigilant when more conspecifics were nearby (Tables 2, 3, 4). Additionally, the day of the year was significant in the first model using the full data set, showing that marmots allocated more time to vigilance as the season progressed (estimate = 0.034, $P < 0.001$; Table 2).

In the July-only data set, the average daily rainfall range was 0.07 cm/d to 0.38 cm/d, and the proportion of days with precipitation ranged from 0.26 to 0.84. None of the weather or climatic variables we tested explained significant variation on the time allocated to foraging. Average daily rainfall in July approached significance (estimate = 0.022, $P = 0.064$; Table 6), suggesting that marmots may allocate more time to foraging as rainfall increases. This effect size was also small (partial- $r_m = 0.0071$, partial- $r_c = 0.2858$; Table 6). Once again, while temperature explained no variation in time allocated to foraging as a main effect (estimate = 0.005, $P = 0.527$; Table 5), the interaction between age class and temperature was significant in explaining variation in foraging time allocation as juveniles foraged less relative to adults as temperatures increased (estimate = -0.040, $P = 0.007$; Table 5). Snowmelt date (estimate = 0.255, $P = 0.134$; Table 5) and proportion of days with rainfall (estimate = 0.013, $P = 0.323$; Table 7) explained no significant variation in the time marmots allocated to foraging. In both the full data set model and the July-limited one, the number of marmots within 10 meters had a significant impact on the proportion of time marmots allocated to foraging during a bout of foraging. Marmots foraged more when more conspecifics were near (Tables 5, 6, 7). In the full data set model, day of year and time of focal also had significant effects on foraging. Marmots appeared to allocate more time to foraging earlier in the season (estimate = -0.023, $P = 0.002$; Table 5) and later in the day (estimate = 0.003, $P = 0.020$; Table 5).

DISCUSSION

Snowmelt date explained significant variation in the proportion of time that marmots allocated to vigilance while foraging but did not affect the proportion of time spent foraging. The age class and temperature interaction (juveniles compared to adults) explained significant variation in the proportion of time allocated to both vigilance and foraging. However, rainfall (both average daily rainfall and proportion of days with rainfall in July) did not explain variation in time allocated to vigilance or foraging. This suggests that seasonality has cross-age class impacts on marmot antipredator behavior while the influence of current weather is more nuanced.

Current weather could affect general activity. For instance, marmots may adjust the amount of total time they spend foraging or the times of day that they forage in response to rising temperatures and changing rain patterns rather than altering their behavior while foraging (the latter of which we have studied extensively). We do not observe marmots under exceptionally hot conditions because they are less active or entirely inactive. This is consistent with behavior of other small mammals such as desert woodrats (*Neotomia lepida*) and northern flying squirrels (*Glaucomys sabrinus*) who alter their active times to avoid or reduce exposure to extreme hot and cold temperatures respectively (Cotton and Parker 2000; Murray and Smith 2012). Pika (*Ochotona princeps*), who live in similar forest-adjacent talus environments to marmots, took refuge in talus burrows to escape the intense heat of a forest fire, which shows the effectiveness of these burrows in sheltering small endotherms from heat and that, behaviorally, these animals take advantage of these resources to thermoregulate (Varner et al. 2015).

As snow melted earlier, marmots allocated more time to vigilance. This could be because earlier snowmelt created a longer growing and active season, which gave marmots more time to grow to their hibernation immergence mass required to survive the winter (Ozgul et al. 2006). Thus, marmots were under less pressure to forage each day, which afforded more time for

vigilance. However, we did not see a reciprocal effect for time allocated to foraging. This may suggest that the increased time devoted to vigilance was not taken from foraging but from other behaviors, such as sitting on rocks or social behavior. Sociality could be impacted if vigilant behavior is increasingly taking precedence over it. Longer active seasons are associated with higher juvenile survival rates, which covaries with overall population growth (Ozgul et al. 2006). The added time for mass gain in extended seasons is especially valuable for smaller animals, such as juveniles and yearlings, as it allows them to grow at a more natural rate rather than undergoing compensatory growth, which can divert energy from maintenance and other biological processes, resulting in decreased survival rates in harsh environmental conditions (Heissenberger et al. 2020). Therefore, increased time allocation to vigilance, in addition to more time across the season for mass gain, could mediate marmot population growth by increasing both summer and winter survival, respectively. Thus, as snow melts earlier with climate change, marmot populations may increase.

When temperatures were higher, juvenile marmots allocated more time to vigilance and less to foraging compared to adults. It is logical that juveniles would be more sensitive to temperature shifts because they are poorer thermoregulators. Juveniles are known to emerge from burrows later in the morning and return to burrows earlier in the afternoon relative to adults to escape more extreme temperatures (Melcher et al. 1990). This was found to be true in our study, too, as the temperature range of juvenile focals was much narrower than that of adults (juvenile temp range = 6.6 °C to 22.9 °C; adult temp range = -0.1 °C to 23.1 °C). The fitness implications of this change in juvenile behavior are unclear without further study. Increased vigilance is likely to increase juvenile summer survival, but decreased foraging could decrease winter survival if juveniles are not able to gain sufficient mass throughout the active season to survive the winter. Juveniles have particularly higher energy requirements in terms of mass gain since they must

grow somatically in addition to gaining fat for the winter (Heissenberger et al. 2020). This potential decrease in winter survival could be neutralized by the longer growing season that comes with earlier snowmelt, but more data must be collected to make this determination. Either way, the impact on juvenile survival is of high importance because juvenile survival is one of the most important determinants of overall marmot population growth (Oli and Armitage 2004).

While the effect of average daily rainfall in July on foraging only approached significance, the July dataset was much smaller than the full data set used for snowmelt and temperature analyses, and the effect size of the almost significant average daily rainfall and foraging association (partial- $r_m = 0.0071$, partial- $r_c = 0.2858$; Table 6) was larger than that of the significant snowmelt and vigilance association (partial- $r_m < 0.0001$, partial- $r_c = 0.208$; Table 2). This suggests that average daily rainfall may have a modest effect on foraging behavior.

As rainfall increased, marmots allocated more time to foraging. This relationship may be best explained by distance to burrow. When there is more rainfall, there is more vegetation close to their burrows, so marmots do not have to travel as far to forage. The Orians and Pearson (1979) central place model predicts that foragers will forage closer to their burrows if predation risk increases as a function of distance to refuge. While distance to burrow did not have a significant effect on proportion of time spent foraging in our model, a large portion of our July focal data lacked distance to burrow estimates, so more data collection could better clarify how risk was incorporated into this decision.

We have confidence in our overall results because several of the fixed effects we included explained variation in time allocated to vigilance and foraging. The directionality of these associations was generally consistent with prior studies and illustrates the energetic and temporal tradeoff between vigilance and foraging. Marmots foraging with more conspecifics were less vigilant and allocated more time to foraging, a common finding across marmot vigilance studies

(Holmes 1984; Carey and Moore 1986; Chmura et al. 2016) and mammalian vigilance studies at large (Quenette 1990). This is likely explained by either the group vigilance or ‘more eyes’ hypothesis (that on the individual level, prey can afford to be less vigilant when they are surrounded by others who are vigilant) or the individual risk hypothesis (that individual predation risk decreases in larger groups due to dilution or confusion effects; thus, less individual vigilance is warranted) (Roberts 1996). Additionally, the models using the full data set found that marmots are more vigilant and forage less later in the season. This is likely due to the cessation of marmot mass gain as early as 3-5 weeks before hibernation, which decreases pressure to forage and affords more time for vigilance (Armitage 2014). In the full data set foraging model, marmots spent a greater proportion of time foraging later in the day. This follows prior research showing that marmots allocated more time to foraging in the afternoons (Armitage et al. 1996). In warmer conditions, yellow-bellied marmots exhibit a bimodal activity cycle with peaks a couple hours after sunrise and around sunset (Pattie 1967). Marmots spend a greater total proportion of the morning active than the afternoon (Armitage et. al 1996), which may result in a need for more concentrated/focused bouts of foraging in the afternoon, thus yielding the trend we see here.

In summary, our significant results predict yellow-bellied marmot population growth in response to climate change as earlier snowmelt creates longer active seasons, which support increased total time spent foraging and increased vigilance per bout of foraging, leading to increased summer and winter survival for marmots of all ages. Juveniles may experience additional survival rate increases with more time allocated to vigilance as temperatures rise and the potential neutralization of decreased time devoted to foraging by the increased length of the growing season. The direct impact of juvenile survival on marmot population growth makes these effects powerful. Further research should be conducted to investigate whether these trends

can be extended to related species and to determine the effects of similar environmental changes on predator behavior to more accurately assess prey population dynamics in response to climate change.

Data were collected with permission from Colorado Parks and Wildlife (TR917, renewed annually) and under the UCLA Institutional Animal Care and Use protocol 2001-191-01 (renewed annually). We thank the many previous marmoteers who have collected these data. We also thank the Rocky Mountain Biological Laboratory for staff and logistical support.

FUNDING

K.A. was supported by the American Society of Mammalogists, a National Science Foundation Graduate Research Fellowship, the RMBL Graduate Fellowship Hunter Endowment, and the University of California Los Angeles. J.G.A.M. was supported by XXX. D.T.B. was supported by the National Geographic Society, the University of California Los Angeles (Faculty Senate and Division of Life Sciences), an RMBL research fellowship, and the U.S. National Science Foundation (NSF IDBR-0754247 and DEB-1119660 and 1557130 to D.T.B., as well as DBI 0242960, 07211346, 1226713, and 1755522 to R.M.B.L.).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Bobb et al. (2024).

REFERENCES

Use APA

Arenz CL, Leger DW. 2000. Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Animal Behaviour*. 59(3):535–541. doi:10.1006/anbe.1999.1345.

Armitage KB. 1962. Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). *Animal Behaviour*. 10(3):319–331. doi:10.1016/0003-3472(62)90055-6.

Armitage KB. 2004. Badger Predation on Yellow-bellied Marmots. *amid*. 151(2):378–387. doi:10.1674/0003-0031(2004)151[0378:BPOYM]2.0.CO;2.

Armitage KB. 2013. Climate change and the conservation of marmots. *NS*. 05(05):36–43. doi:10.4236/ns.2013.55A005.

Armitage KB. 2014. *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*. University Printing House, Cambridge CB2 8BS, United Kingdom: Cambridge University Press.

Armitage KB, Salsbury CM, Barthelmess EL, Gray RC, Kovach A. 1996. Population time budget for the yellow-bellied marmot. *Ethology Ecology & Evolution*. 8(1):67–95. doi:10.1080/08927014.1996.9522936.

Bachman GC. 1993. The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. *Animal Behaviour*. 46(2):233–244. doi:10.1006/anbe.1993.1185.

barr billy. 2002. Gothic Weather. [accessed 2024 Aug 2]. <https://www.gothicwx.org/>.

Beale PK, Marsh KJ, Foley WJ, Moore BD. 2018. A hot lunch for herbivores: physiological effects of elevated temperatures on mammalian feeding ecology. *Biological Reviews*. 93(1):674–692. doi:10.1111/brv.12364.

Beauchamp G, Li Z, Yu C, Bednekoff PA, Blumstein DT. 2021. A meta-analysis of the group-size effect on vigilance in mammals. *Behavioral Ecology*. 32(5):919–925. doi:10.1093/beheco/arab048.

Bednekoff PA, Blumstein DT. 2009. Peripheral obstructions influence marmot vigilance: integrating observational and experimental results. *Behavioral Ecology*. 20(5):1111–1117. doi:10.1093/beheco/arp104.

Beever EA, Hall LE, Varner J, Loosen AE, Dunham JB, Gahl MK, Smith FA, Lawler JJ. 2017. Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment*. 15(6):299–308. doi:10.1002/fee.1502.

Biro PA, Beckmann C, Stamps JA. 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proc Biol Sci*. 277(1678):71–77. doi:10.1098/rspb.2009.1346.

Biro PA, O'Connor J, Pedini L, Gribben PE. 2013. Personality and plasticity: consistent responses within-, but not across-temperature situations in crabs. *Behaviour*. 150(7):799–811.

Blumstein DT, Cooley L, Winternitz J, Daniel JC. 2008. Do yellow-bellied marmots respond to predator vocalizations? *Behav Ecol Sociobiol.* 62(3):457–468. doi:10.1007/s00265-007-0473-4.

Blumstein DT, Daniel JC. 2004. Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles. *Animal Behaviour.* 68(6):1257–1265. doi:10.1016/j.anbehav.2003.12.024.

Blumstein DT, Ozgul A, Yovovich V, Van Vuren DH, Armitage KB. 2006. Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. *Journal of Zoology.* 270(1):132–138. doi:10.1111/j.1469-7998.2006.00098.x.

Blumstein DT, Runyan A, Seymour M, Nicodemus A, Ozgul A, Ransler F, Im S, Stark T, Zugmeyer C, Daniel JC. 2004. Locomotor Ability and Wariness in Yellow-Bellied Marmots. *Ethology.* 110(8):615–634. doi:10.1111/j.1439-0310.2004.01000.x.

Bolinger R, Lukas J, Schumacher R, Goble P. 2023. Climate change in Colorado. [accessed 2024 May 25]. <https://hdl.handle.net/10217/237323>.

Boyles JG, Seebacher F, Smit B, McKechnie AE. 2011. Adaptive Thermoregulation in Endotherms May Alter Responses to Climate Change. *Integrative and Comparative Biology.* 51(5):676–690. doi:10.1093/icb/icer053.

Briffa M, Bridger D, Biro PA. 2013. How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. *Animal Behaviour.* 86(1):47–54. doi:10.1016/j.anbehav.2013.04.009.

Buchholz R, Banusiewicz JD, Burgess S, Crocker-Buta S, Eveland L, Fuller L. 2019. Behavioural research priorities for the study of animal response to climate change. *Animal Behaviour.* 150:127–137. doi:10.1016/j.anbehav.2019.02.005.

Calvin K, Dasgupta D, Krinner G, Mukherji A, Thorne PW, Trisos C, Romero J, Aldunce P, Barrett K, Blanco G, et al. 2023. IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. First. Intergovernmental Panel on Climate Change (IPCC). [accessed 2024 Jun 13]. <https://www.ipcc.ch/report/ar6/syr/>.

Carey HV, Moore P. 1986. Foraging and Predation Risk in Yellow-Bellied Marmots. *The American Midland Naturalist.* 116(2):267–275. doi:10.2307/2425734.

Chmura HE, Wey TW, Blumstein DT. 2016. Assessing the sensitivity of foraging and vigilance to internal state and environmental variables in yellow-bellied marmots (*Marmota flaviventris*). *Behav Ecol Sociobiol.* 70(11):1901–1910. doi:10.1007/s00265-016-2195-y.

Cockrem JF. 2022. Individual variation, personality, and the ability of animals to cope with climate change. *Front Ecol Evol.* 10. doi:10.3389/fevo.2022.897314. [accessed 2024 Jun 18]. <https://www.frontiersin.org/articles/10.3389/fevo.2022.897314>.

Comstock JP, Ehleringer JR. 1992. Plant Adaptation in the Great Basin and Colorado Plateau. *The Great Basin Naturalist.* 52(3):195–215.

Cooper CE, Withers PC, Hurley LL, Griffith SC. 2019. The Field Metabolic Rate, Water Turnover, and Feeding and Drinking Behavior of a Small Avian Desert Granivore During a Summer Heatwave. *Front*

- Physiol. 10. doi:10.3389/fphys.2019.01405. [accessed 2024 May 30].
<https://www.frontiersin.org/journals/physiology/articles/10.3389/fphys.2019.01405/full>.
- Cotton CL, Parker KL. 2000. Winter activity patterns of northern flying squirrels in sub-boreal forests. *Can J Zool.* 78(11):1896–1901. doi:10.1139/z00-137.
- Crane AL, Fritts AK, Mathis A, Lisek JC, Barnhart MC. 2011. Do gill parasites influence the foraging and antipredator behaviour of rainbow darters, *Etheostoma caeruleum*? *Animal Behaviour.* 82(4):817–823. doi:10.1016/j.anbehav.2011.07.015.
- Curio E. 2012. *The Ethology of Predation.* Springer Science & Business Media.
- Dammhahn M, Almeling L. 2012. Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Animal Behaviour.* 84(5):1131–1139. doi:10.1016/j.anbehav.2012.08.014.
- Di Blanco Y, Hirsch BT. 2006. Determinants of vigilance behavior in the ring-tailed coati (*Nasua nasua*): the importance of within-group spatial position. *Behav Ecol Sociobiol.* 61(2):173–182. doi:10.1007/s00265-006-0248-3.
- Dunbar RIM, Korstjens AH, Lehmann J, Project BACR. 2009. Time as an ecological constraint. *Biological Reviews.* 84(3):413–429. doi:10.1111/j.1469-185X.2009.00080.x.
- Feldhamer GA, Thompson BC, Chapman JA. 2003. *Wild Mammals of North America: Biology, Management, and Conservation.* JHU Press.
- Fuller A, Dawson T, Helmuth B, Hetem RS, Mitchell D, Maloney SK. 2010. Physiological Mechanisms in Coping with Climate Change. *Physiological and Biochemical Zoology.* 83(5):713–720. doi:10.1086/652242.
- Funghi C, McCowan LSC, Schuett W, Griffith SC. 2019. High air temperatures induce temporal, spatial and social changes in the foraging behaviour of wild zebra finches. *Animal Behaviour.* 149:33–43. doi:10.1016/j.anbehav.2019.01.004.
- Gomes FR, Bevier CR, Navas CA. 2002. Environmental and Physiological Factors Influence Antipredator Behavior in *Scinax hiemalis* (Anura: Hylidae). Gatten Jr. RE, editor. *Copeia.* 2002(4):994–1005. doi:10.1643/0045-8511(2002)002[0994:EAPFIA]2.0.CO;2.
- Gothic Weather. Gothic Weather. [accessed 2024 Jul 4]. <https://www.gothicwx.org/>.
- Heissenberger S, De Pinho GM, Martin JGA, Blumstein DT. 2020. Age and location influence the costs of compensatory and accelerated growth in a hibernating mammal. Simmons L, editor. *Behavioral Ecology.* 31(3):826–833. doi:10.1093/beheco/araa013.
- Hetem RS, Mitchell D, De Witt BA, Fick LG, Maloney SK, Meyer LCR, Fuller A. 2019. Body temperature, activity patterns and hunting in free-living cheetah: biologging reveals new insights. *Integrative Zoology.* 14(1):30–47. doi:10.1111/1749-4877.12341.
- Holmes WG. 1984. Predation risk and foraging behavior of the hoary marmot in Alaska. *Behav Ecol Sociobiol.* 15(4):293–301. doi:10.1007/BF00292992.
- Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation.

- Philosophical Transactions of the Royal Society B: Biological Sciences. 367(1596):1665–1679. doi:10.1098/rstb.2012.0005.
- Ives AR, Dobson AP. 1987 Sep 1. Antipredator Behavior and the Population Dynamics of Simple Predator-Prey Systems. *The American Naturalist*. doi:10.1086/284719. [accessed 2024 Jul 30]. <https://www.journals.uchicago.edu/doi/10.1086/284719>.
- Lea AJ, Blumstein DT. 2011a. Ontogenetic and Sex Differences Influence Alarm Call Responses in Mammals: a Meta-Analysis. *Ethology*. 117(10):839–851. doi:10.1111/j.1439-0310.2011.01947.x.
- Lea AJ, Blumstein DT. 2011b. Age and sex influence marmot antipredator behavior during periods of heightened risk. *Behav Ecol Sociobiol*. 65(8):1525–1533. doi:10.1007/s00265-011-1162-x.
- Lenihan C, Vuren DV. 1996. Growth and survival of juvenile yellow-bellied marmots (*Marmota flaviventris*). *Can J Zool*. 74(2):297–302. doi:10.1139/z96-037.
- Lienart GDH, Mitchell MD, Ferrari MCO, McCormick MI. 2014. Temperature and food availability affect risk assessment in an ectotherm. *Animal Behaviour*. 89:199–204. doi:10.1016/j.anbehav.2013.12.031.
- Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*. 16(5):945–956. doi:10.1093/beheco/ari075.
- Mady RP, Blumstein DT. 2017. Social security: are socially connected individuals less vigilant? *Animal Behaviour*. 134:79–85. doi:10.1016/j.anbehav.2017.10.010.
- Mateo JM. 2007. Ecological and hormonal correlates of antipredator behavior in adult Belding's ground squirrels (*Spermophilus beldingi*). *Behav Ecol Sociobiol*. 62(1):37–49. doi:10.1007/s00265-007-0436-9.
- McCoy AL, Jacobs KL, Vano JA, Wilson JK, Martin S, Pendergrass AG, Cifelli R. 2022. The Press and Pulse of Climate Change: Extreme Events in the Colorado River Basin. *JAWRA Journal of the American Water Resources Association*. 58(6):1076–1097. doi:10.1111/1752-1688.13021.
- Melcher JC, Armitage KB, Porter WP. 1990. Thermal Influences on the Activity and Energetics of Yellow-Bellied Marmots (*Marmota flaviventris*). *Physiological Zoology*. 63(4):803–820.
- Mella VSA, Cooper CE, Karr M, Krockenberger A, Madani G, Webb EB, Krockenberger MB. 2024. Hot climate, hot koalas: the role of weather, behaviour and disease on thermoregulation. *Conservation Physiology*. 12(1):coae032. doi:10.1093/conphys/coae032.
- Monclús R, Anderson AM, Blumstein DT. 2015. Do Yellow-Bellied Marmots Perceive Enhanced Predation Risk When they are Farther from safety? An experimental study. *Ethology*. 121(9):831–839. doi:10.1111/eth.12397.
- Mori A, Burghardt GM. 2004. THERMAL EFFECTS ON THE ANTIPREDATOR BEHAVIOUR OF SNAKES: A REVIEW AND PROPOSED TERMINOLOGY.
- Moss JB, While GM. 2021. The thermal environment as a moderator of social evolution. *Biological Reviews*. 96(6):2890–2910. doi:10.1111/brv.12784.
- Murray IW, Smith FA. 2012. Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies. *Can J Zool*. 90(9):1171–1180. doi:10.1139/z2012-084.

Oli MK, Armitage KB. 2004. Yellow-Bellied Marmot Population Dynamics: Demographic Mechanisms of Growth and Decline. *Ecology*. 85(9):2446–2455.

Ozgul A, Armitage KB, Blumstein DT, Oli MK. 2006. SPATIOTEMPORAL VARIATION IN SURVIVAL RATES: IMPLICATIONS FOR POPULATION DYNAMICS OF YELLOW-BELLIED MARMOTS. *Ecology*. 87(4):1027–1037. doi:10.1890/0012-9658(2006)87[1027:SVISRI]2.0.CO;2.

Perrin N, Sibly RM. 1993. Dynamic Models of Energy Allocation and Investment. *Annual Review of Ecology, Evolution, and Systematics*. 24(Volume 24, 1993):379–410. doi:10.1146/annurev.es.24.110193.002115.

Pollard KA, Blumstein DT. 2008. Time allocation and the evolution of group size. *Animal Behaviour*. 76(5):1683–1699. doi:10.1016/j.anbehav.2008.08.006.

Pruitt JN, Demes KW, Dittrich-Reed DR. 2011. Temperature Mediates Shifts in Individual Aggressiveness, Activity Level, and Social Behavior in a Spider. *Ethology*. 117(4):318–325. doi:10.1111/j.1439-0310.2011.01877.x.

Quenette P-Y. 1990. Functions of vigilance behavior in mammals: a review. *Acta Oecologica*. 11:801–818.

Roberts G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour*. 51(5):1077–1086. doi:10.1006/anbe.1996.0109.

Rocky Mountain Biological Laboratory. 2002. RMBL Spatial Data Platform. [accessed 2024 Aug 2]. <https://www.rmbll.org/scientists/resources/spatial-data-platform/>.

Rogers SA, Robbins CT, Mathewson PD, Carnahan AM, van Manen FT, Haroldson MA, Porter WP, Rogers TR, Soule T, Long RA. 2021. Thermal constraints on energy balance, behaviour and spatial distribution of grizzly bears. *Functional Ecology*. 35(2):398–410. doi:10.1111/1365-2435.13727.

Soravia C. 2022. Investigating the relationship between heat stress and cognition in a wild animal. University of Western Australia. [accessed 2024 May 24]. https://api.research-repository.uwa.edu.au/ws/portalfiles/portal/247402607/THESIS_DOCTOR_OF_PHILOSOPHY_SORAVIA_Camilla_2023.pdf.

Soravia C, Ashton BJ, Thornton A, Bourne AR, Ridley AR. 2024. High temperatures during early development reduce adult cognitive performance and reproductive success in a wild animal population. *Science of The Total Environment*. 912:169111. doi:10.1016/j.scitotenv.2023.169111.

Soravia C, Ashton BJ, Thornton A, Ridley AR. 2023. High temperatures are associated with reduced cognitive performance in wild southern pied babblers. *Proceedings of the Royal Society B: Biological Sciences*. 290(2011):20231077. doi:10.1098/rspb.2023.1077.

Stamps JA. 2007. Growth-mortality tradeoffs and ‘personality traits’ in animals. *Ecol Lett*. 10(5):355–363. doi:10.1111/j.1461-0248.2007.01034.x.

Stankowich T, Blumstein DT. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*. 272(1581):2627–2634. doi:10.1098/rspb.2005.3251.

Uchida K, Blumstein DT. 2021. Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance. *Behavioral Ecology*. 32(4):668–678. doi:10.1093/beheco/arab016.

Varner J, Lambert MS, Horns JJ, Lavery S, Disney L, Beever EA, Dearing MD. 2015. Too hot to trot? Evaluating the effects of wildfire on patterns of occupancy and abundance for a climate-sensitive habitat specialist. *Int J Wildland Fire*. 24(7):921–932. doi:10.1071/WF15038.

Vuren DHV. 2001. Predation on Yellow-bellied Marmots (*Marmota flaviventris*). *Amid*. 145(1):94–100. doi:10.1674/0003-0031(2001)145[0094:POYBMM]2.0.CO;2.

Vuren DV. 1991. Yellow-bellied Marmots as Prey of Coyotes. *American Midland Naturalist*. 125(1):135. doi:10.2307/2426376.

Vuren DV, Armitage KB. 1991. Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. *Can J Zool*. 69(7):1755–1758. doi:10.1139/z91-244.

Weetman D, Atkinson D, Chubb JC. 1998. Effects of temperature on anti-predator behaviour in the guppy, *Poecilia reticulata*. *Animal Behaviour*. 55(5):1361–1372. doi:10.1006/anbe.1997.0666.

Weiner J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: Ecological implications. *Trends in Ecology & Evolution*. 7(11):384–388. doi:10.1016/0169-5347(92)90009-Z.

Table 1. Behaviors scored during a foraging focal (Chmura et al. 2016).

Behavior	Description
Stand forage (f)	The marmot was on all four legs with its mouth towards the vegetation and head down.
Rear forage (g)	The marmot stood on its hind legs and ingested vegetation.
Stand look (l)	The marmot was on all four legs with its head up, looking.
Rear look (r)	The marmot stood on its hind legs only with its head up, looking.
Walk (w)	The marmot walked.
Run (n)	The marmot ran.
Out-of-sight (o)	The marmot was out of the view of the observer.
Other (t)	The marmot did something other than the actions described above (e.g., participating in a social interaction).

Table 2. Results of linear mixed effects model 1. Snowmelt date and temperature effects on time allocated to vigilance while foraging by marmots.

	Variable	Estimate	SE	P-value	Partial Marginal Effect Size	Partial Conditional Effect Size
Fixed effects						
	Snowmelt	-0.002	<0.001	0.037	0.000	0.208
	Temperature	-0.008	0.007	0.281	0.000	0.218
	Valley Up	-0.072	0.039	0.102	0.032	0.250
	Day of Year	0.034	0.007	<0.001	0.008	0.226
	Time of Focal	-0.002	0.001	0.105	0.007	0.224
	Marmots within 10 meters	-0.017	0.004	<0.001	0.006	0.224
	Substrate LVD	0.009	0.011	0.375	0.000	0.218
	Substrate ST	<0.001	0.026	0.957	0.000	0.218
	Juvenile Age Class	-0.180	0.020	<0.001	0.052	0.270
	Yearling Age Class	-0.015	0.012	0.196	0.052	0.270
	Male Sex	-0.008	0.011	0.426	0.001	0.219
	Age Class * Temperature	0.033	0.014	0.017	0.046	0.263
Random effects						
		Variance	SD			
	UID	0.002	0.047			
	Year	0.002	0.042			
	Colony	0.003	0.055			

Table 3. Results of linear mixed effects model 2. July average daily rainfall's effect on time allocated to vigilance while foraging by marmots.

	Variable	Estimate	SE	P-value	Partial Marginal Effect Size	Partial Conditional Effect Size
Fixed effects						
	Daily Average Rainfall (July)	-0.013	0.013	0.329	0.000	0.368
	Valley Up	-0.061	0.050	0.287	0.007	0.376
	Day of Year	0.007	0.013	0.609	0.000	0.368
	Time of Focal	<-0.001	0.003	0.990	0.000	0.369
	Marmots within 10 meters	-0.030	0.013	0.021	0.018	0.387
	Substrate LVD	0.014	0.024	0.563	0.000	0.366
	Substrate ST	0.028	0.053	0.606	0.000	0.366
	Juvenile Age Class	-0.148	0.035	<0.001	0.119	0.487
	Yearling Age Class	-0.012	0.038	0.743	0.119	0.487
	Male Sex	-0.011	0.029	0.700	0.001	0.369
Random effects						
		Variance	SD			
	UID	0.012	0.108			
	Year	0.001	0.026			
	Colony	0.002	0.050			

Table 4. Results of linear mixed effects model 3. The proportion of days with rainfall in July's effect on time allocated to vigilance while foraging by marmots.

	Variable	Estimate	SE	P-value	Partial Marginal Effect Size	Partial Conditional Effect Size
Fixed effects						
	Proportion of Days with Rainfall (July)	-0.003	0.013	0.821	0.001	0.383
	Valley Up	-0.060	0.013	0.311	0.006	0.389
	Day of Year	0.006	0.013	0.653	0.000	0.382
	Time of Focal	<-0.001	0.003	0.955	0.000	0.383
	Marmots within 10 meters	-0.031	0.013	0.018	0.021	0.403
	Substrate LVD	0.012	0.024	0.597	0.000	0.379
	Substrate ST	0.025	0.054	0.638	0.000	0.379
	Juvenile Age Class	-0.146	0.035	<0.001	0.119	0.501
	Yearling Age Class	-0.015	0.038	0.704	0.119	0.501
	Male Sex	-0.009	0.029	0.746	0.001	0.383
Random effects						
		Variance	SD			
	UID	0.012	0.109			
	Year	0.001	0.028			
	Colony	0.003	0.055			

Table 5. Results of linear mixed effects model 4. Snowmelt date and temperature effects on time allocated to foraging during a bout of foraging by marmots.

	Variable	Estimate	SE	P-value	Partial Marginal Effect Size	Partial Conditional Effect Size
Fixed effects						
	Snowmelt	0.255	0.134	0.072	0.000	0.185
	Temperature	0.005	0.007	0.527	0.000	0.179
	Valley Up	0.096	0.042	0.058	0.000	0.195
	Day of Year	-0.027	0.008	<0.001	0.000	0.182
	Time of Focal	0.003	0.001	0.018	0.000	0.181
	Marmots within 10 meters	0.014	0.005	0.002	0.000	0.200
	Substrate LVD	-0.012	0.016	0.285	0.000	0.182
	Substrate ST	-0.031	0.027	0.252	0.000	0.182
	Juvenile Age Class	0.169	0.021	<0.001	0.014	0.240
	Yearling Age Class	0.016	0.012	0.185	0.014	0.240
	Male Sex	0.013	0.011	0.238	0.000	0.183
	Age Class (Juvenile) * Temperature	-0.040	0.015	0.007	0.056	0.281
Random effects						
		Variance	SD			
	UID	0.002	0.045			
	Year	0.003	0.052			
	Colony	0.004	0.059			

Table 6. Results of linear mixed effects model 5. July average daily rainfall's effect on time allocated to foraging during a bout of foraging by marmots.

	Variable	Estimate	SE	P-value	Partial Marginal Effect Size	Partial Conditional Effect Size
Fixed effects						
	Daily Average Rainfall (July)	0.022	0.012	0.064	0.007	0.286
	Valley Up	0.102	0.057	0.144	0.021	0.300
	Day of Year	0.005	0.014	0.714	0.001	0.280
	Time of Focal	<0.001	0.003	0.941	0.000	0.279
	Marmots within 10 meters	0.027	0.013	0.046	0.016	0.294
	Substrate LVD	-0.019	0.024	0.432	0.004	0.282
	Substrate ST	-0.062	0.057	0.729	0.004	0.282
	Juvenile Age Class	0.111	0.035	0.002	0.082	0.361
	Yearling Age Class	0.028	0.039	0.467	0.082	0.361
	Male Sex	0.025	0.029	0.878	0.003	0.282
Random effects						
		Variance	SD			
	UID	0.008	0.088			
	Year	0.004	0.063			
	Colony	0.024	0.154			

Table 7. Results of linear mixed effects model 7. The proportion of days with rainfall in July's effect on time allocated to foraging during a bout of foraging by marmots.

	Variable	Estimate	SE	P-value	Partial Marginal Effect Size	Partial Conditional Effect Size
Fixed effects						
	Proportion of Days with Rainfall (July)	0.013	0.013	0.323	0.004	0.303
	Valley Up	0.106	0.060	0.145	0.020	0.320
	Day of Year	0.007	0.014	0.520	0.001	0.301
	Time of Focal	<0.001	0.003	0.833	0.001	0.301
	Marmots within 10 meters	0.027	0.014	0.049	0.015	0.315
	Substrate LVD	-0.016	0.025	0.521	0.000	0.300
	Substrate ST	-0.060	0.058	0.305	0.000	0.300
	Juvenile Age Class	0.107	0.036	0.003	0.082	0.382
	Yearling Age Class	0.027	0.040	0.502	0.082	0.382
	Male Sex	0.029	0.029	0.311	0.002	0.302
Random effects						
		Variance	SD			
	UID	0.008	0.088			
	Year	0.000	0.019			
	Colony	0.005	0.068			

Figure Legends

Fig. 1. Weather and climate variables' effects on time marmots allocate to vigilance while foraging. All variables were scaled (root mean squared). The circles represent individual observations, and the lines and shaded regions represent lines of best fit and margins of error with a 95% confidence interval. Snowmelt date had a significant effect on marmot vigilance while foraging. When snow melted earlier, marmots were less vigilant. The effect size is very small ($\text{partial-}r_m < 0.0001$). The temperature and age class interactions were significant in explaining variation in time allocated to vigilance. As temperatures increased, juveniles allocated more time to vigilance. This effect size was larger but still small ($\text{partial-}r_m = 0.046$).

Fig. 2. Weather and climate variables' effects on time marmots allocate to foraging during a bout of foraging. All variables were scaled (root mean squared). The circles represent individual observations, and the lines and shaded regions represent lines of best fit and margins of error with a 95% confidence interval. The temperature and age class interactions were significant in explaining variation in time allocated to foraging. As temperatures increased, juveniles allocated less time to foraging. This effect size was similar to the temperature-age-class and vigilance effect size from Fig. 1 ($\text{partial-}r_m = 0.056$).



