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**Investigating the role of climate on juvenile Golden-mantled ground squirrel
(*Callospermophilus lateralis*) growth and behavior**

Abstract

Changes to climate can have a variety of consequences on organisms across all taxa. Though we are seeing climate changes across the globe, these effects can often be greater in high-elevation regions. For mammals in these environments, climate change can alter phenology, survival, and reproduction. Increasing temperatures have also been found to affect body mass, though this has been inadequately explored. This study investigated the effects of climate on the body mass and behavior of a high-elevation, hibernating small mammal, the golden-mantled ground squirrel (*Callospermophilus lateralis*). We compared the temperature and precipitation faced during a critical two-week growth period in juvenile ground squirrels to daily growth rates to determine any effects of climatic conditions on development. Additionally, we monitored juvenile squirrel behavior to compare time spent above ground and foraging to the temperature during that time. We found that temperature does significantly negatively affect time spent above ground and foraging, and that number of days with rain during the growth period was a significant negative predictor of growth rate. Furthermore, the number of days over 25 °C was a significant positive predictor of growth rate. Additionally, we found that year and maternal ID

accounted for up 15% and 30% of the variation in growth rate, respectively. Together, these results aid in our understanding of how climate and other variables can affect body mass and behavior in small mammals.

Introduction

As climate warms and changes, we are seeing widespread effects across organisms in all environments. From decreases in body size (Sheridan et al. 2011), to mismatches in phenology and behavior (Chmura et al. 2023) to shifts in predator-prey dynamics (Bastille-Rousseau et al. 2018), changes to climate are proving to be challenging for organisms across the globe. Pair these changes with the significant relationship between rapid warming and population declines in both birds and mammals (Spooner et al. 2018), and it is evident climate change effects should continue to be a focus for environmental scientists.

Though we are seeing changes in climate globally, mountain regions are considered climate hotspots due to their potential to experience exacerbated changes in climate and the domino effects that can have on lower elevations (Pepin et al. 2022). Previous climate studies have found a general trend of greater warming at high altitudes (Trenberth et al. 2007). This can have potentially dramatic effects on high-elevation animals adapted to specific environments. For example, rising temperatures in mountain regions can shift organisms further up the mountain to maintain their desired climate, which can lead to greater levels of competition and eventually extinction for some species (Urban, 2018). Not all responses to climate change are inherently negative, however, and increasing temperatures could have mixed or positive effects on survival in some species (Cordes et al. 2020).

The effects of climate and thermal environment on most ectotherms are widely studied. For example, previous studies on rainbow trout and Chinook salmon found higher temperatures increased juvenile growth rates (Beer & Anderson. 2011), while a study on multiple tadpole species found greater daily temperature fluctuations decreased growth rates (Kern et al. 2018). However, there is a lack of focus on these topics in mammals. In hibernating mammals specifically, previous studies have identified shifts in phenology and survival rates in response to changes to climate (Lane et al. 2012, Cordes et al. 2020), though consequences of climatic changes on body mass and condition have been minimally studied in comparison within this field of mammal research (Wells et al. 2022).

The golden-mantled ground squirrel (*Callospermophilus lateralis*), or GMGS hereafter, is a small, hibernating, high-elevation mammal. Litters are conceived in spring and come aboveground for the first time at weaning roughly two months later from early June to August. Once pups emerge, they have around two to six weeks to forage and grow before they disperse away from their natal home range. This short stage in juvenile development is critical for surviving through hibernation, with pre-hibernation body mass positively correlating with overwinter survival (Howland et al. 2024). Pups nearly double in size during the first two weeks of rapid development, but daily growth rates vary significantly between individuals (Wells, *in prep*). The factors driving these differences in growth, however, have not been fully explored.

Current research shows that growth rates are declining for GMGS pups born later in the summer (Wells & Van Vuren, 2018), and temperatures and precipitation generally increase later in the summer, but a connection between these two things has yet to be made. Therefore, by comparing archival data of GMGS growth rates with the temperature and precipitation faced during their growing period, we developed a model to determine if either temperature or precipitation has a significant effect on GMGS development. Additionally, we conducted

behavioral observations of juveniles during this summer's growing period to see if climate variables significantly affected their behavior in terms of time spent above ground and time spent foraging. Generally, we expected to see a decrease in above ground and foraging behavior and growth rate if temperatures or precipitation levels are high during the post wean period, as these variables could limit opportunities to forage and increase energy use for thermoregulation.

Methods

For this study, I used climate and growth rate data collected from 2018-2023 at the Rocky Mountain Biological Laboratory in Gothic, Colorado. Climate data was collected by the Gothic weather station AN097, which took hourly temperature every day during the study period, and from RMBL resident, Billy Barr, who took daily precipitation values during the entirety of the study. Hourly temperature data was only pulled from 7am to 6pm, as personal observation found this to be the active period for pups. Precipitation data was a daily total in inches that accounted for rain faced during any time of day. Pup growth data was collected through trapping and weighing of pups using a Pesola spring scale to measure mass to the nearest 1g (Howland et al. 2024). All pups were located within the Gothic townsite. Burrows were located by observing reproductive female home ranges and searching for pups. Pups were captured between June and August at date of emergence from burrow using walk-in traps (5"x5" Tomahawk) baited with a peanut butter and sunflower seed mix. In addition to weight, the time and place of capture was recorded. Pups were uniquely marked with a permanent dye and ear tagged with a unique number code for individual identification. Anal-genital distance was measured to determine sex (Howland et al. 2024). Pups were targeted for recapture 2 weeks after emergence (range 11-18 days) and reweighed. Growth rate was determined by dividing the total mass gained by the

number of days between first and second capture. Throughout the 5 years, 129 pups had their growth rates recorded.

To see how climate could be affecting juvenile growth, I constructed a linear mixed effects model to predict juvenile mass change per day as function of precipitation and temperature. I modeled six fixed effects: days since bare ground, total precipitation, number of days with rain, average daily sum temperature, number of days over 25 degrees Celsius, and maternal age. Days since bare ground was defined as how many days had it been since the last day of snow, which indicates the start of the growing season (Van Vuren & Armitage, 1991). Total precipitation was calculated in total inches of rain recorded during the growth period. Number of days with rain was defined by how many days during the growth period had greater than zero inches of rain, as measured by a rain gauge. Average daily sum temperature was calculated by summing the hourly temperature in Celsius for each day during the growth period, then adding them up and dividing by the number of days. This method accounted for more temperature variation than average alone, as there was little variation in daily averages, but greater variation in the daily sums. The number of days over 25 degrees Celsius was defined as how many days during the growth period reached over 25 degrees Celsius within the 7am to 6pm time frame. 25 degrees Celsius was used as a cutoff high temperature because this temperature was found to reduce above ground activity in another high-elevation, ground-dwelling species, the alpine marmot, *Marmota marmota* (Turk & Arnold, 1984). Maternal age was coded into two categories: yearling, meaning only 1 year old, or older than yearling, meaning any age greater than 1 year. Maternal ID and year were included as random effects to account for unmeasured variation among years and mothers.

For behavioral observations, pups were monitored for 10 minutes every hour from 8am to 6pm during the two-week growth period. The number of pups seen above ground (maximum

litter size $n=7$), individual ID, and individual behaviors were recorded (Ferron, 1985). A Pearson's correlation was used to compare the temperature to the number of pups seen above ground, and a generalized linear model with Poisson distribution was constructed to determine the effects of temperature versus time of day on the number of pups above ground. Time of day was centered around noon and values were squared to account for a more accurate representation of expected above ground pup behavior, since pups typically have active periods both in the morning and again in the afternoon. A binomial generalized linear model was constructed to evaluate the effect of temperature on foraging behavior (i.e. foraging or not). Because previous work has found higher temperatures resulting in decreased activity in another ground squirrel, the alpine marmot, (Turk & Arnold, 1984), we expected to see a similar trend with the GMGS, with greater temperatures resulting in less above ground and foraging activity. All estimates are reported ± 1 standard error.

Results

In terms of the relationship between behavior and temperature, a Pearson's's product correlation showed a significant, moderately negative relationship between temperature and the number of pups above ground ($r = 0.40$, $p = 0.00014$). Additionally, a linear model using temperature and time of day as predictors for number of pups above ground showed temperature had a stronger and more reliable effect ($\beta = -0.046 \pm 0.030$, $z\text{-value} = -1.56$) on number of pups above ground than time ($\beta = -0.033 \pm 0.042$, $z\text{-value} = -0.79$). A binomial generalized linear model using temperature as a predictor of foraging found a significant negative effect of temperature on whether or not a pup was foraging ($\beta = -0.14 \pm 0.066$, $p = 0.040$).

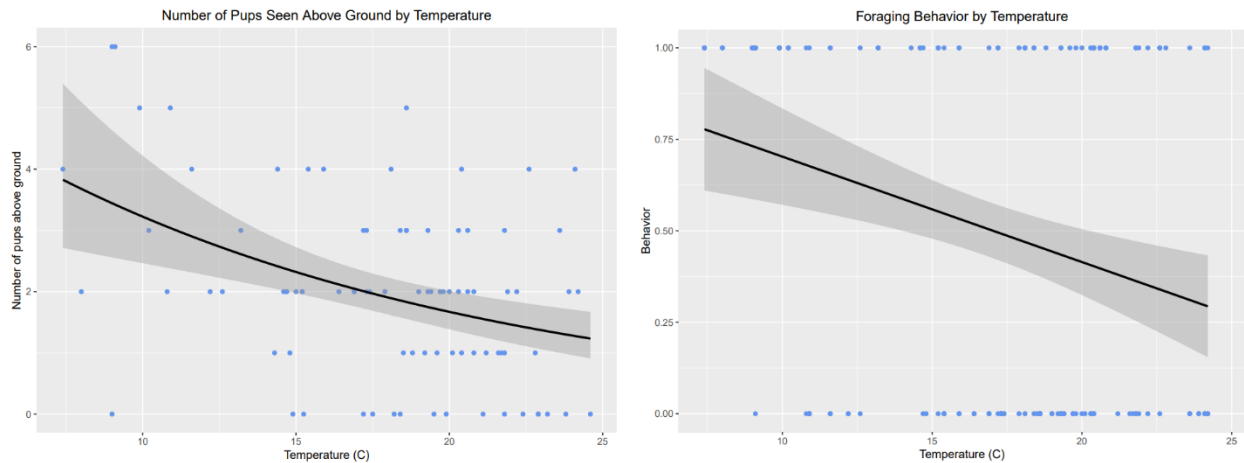


Figure 1. Relationship between temperature and above ground behavior. The left figure compares the number of pups seen above ground during an observation period with the temperature during that time. The right figure shows observed pup behavior (coded as 1 for foraging or 0 for other) compared with the temperature during the observation period.

For growth rates, we found significant differences between years and between different mothers. Overall, growth rates ranged from 1.2 grams per day to 6 grams per day, with an average of 3.23 grams per day. Growth rate averages varied by year, with 2018 having the highest average growth rate of 3.8 grams per day, and 2022 having the lowest average growth rate of 2.9 grams per day. Growth rates have overall been decreasing over the years, but there was no notable increasing or decreasing patterns in temperature or precipitation during the study. Growth rates also varied greatly by maternal ID. Averaging growth rates for moms across the six years, mass change per day ranged from 3.92 grams to as little as 1.59 grams.

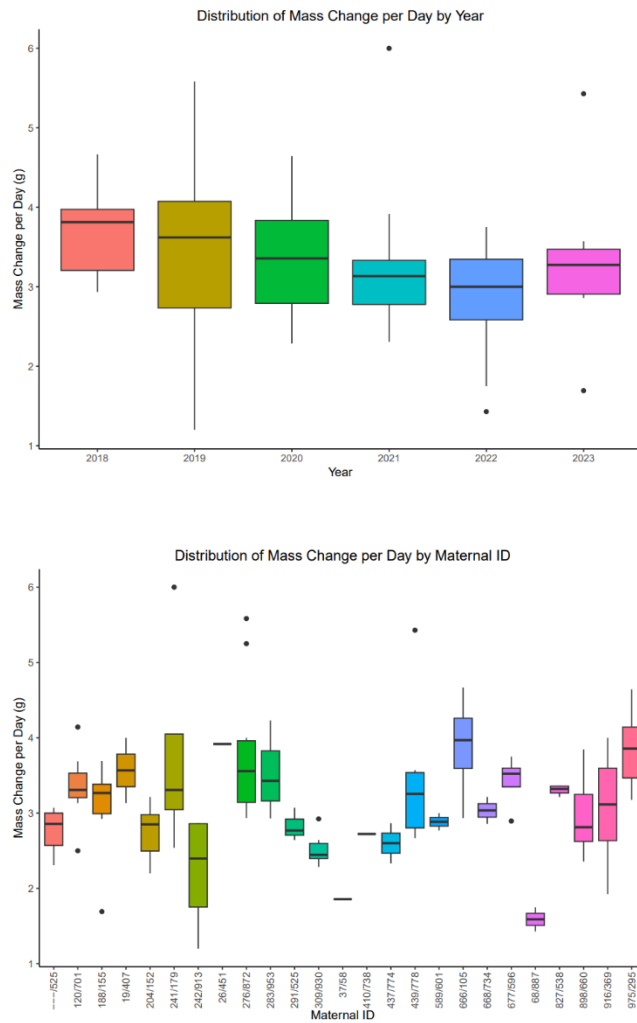


Figure 2. Differences in growth rates between years and from different mothers. The top figure shows average mass change per day across all pups during that year. The bottom figure shows average mass change per day across all pups from the same mother during the six years of study.

The results of the linear mixed model showed that temperature and precipitation had variable effects on juvenile daily growth rate. There were two reliable, significant predictors for growth rate determined by our model: Number of days with rain and number of days over 25 °C. Interestingly, the average sum daily temperature had insignificant effects on growth rate ($\beta = -0.0023 \pm 0.0030$, t -value = -0.77), but days over 25 degrees Celsius had a reliably positive effect on growth rate, and was the strongest predictor of growth rate in the model ($\beta = 0.40 \pm 0.17$, t -

value = 2.32). Number of days with rain during the growth period was a significant negative predictor of growth rate ($\beta = -0.09 \pm 0.04$, t-value = -2.26). Total precipitation did not have any significant effects on growth rate ($\beta = 0.23 \pm 0.24$, t-value = 0.96). Days since bareground and maternal age were not significant predictors. Maternal ID accounted for 30% of variance in growth rate, and year accounted for another 15%.

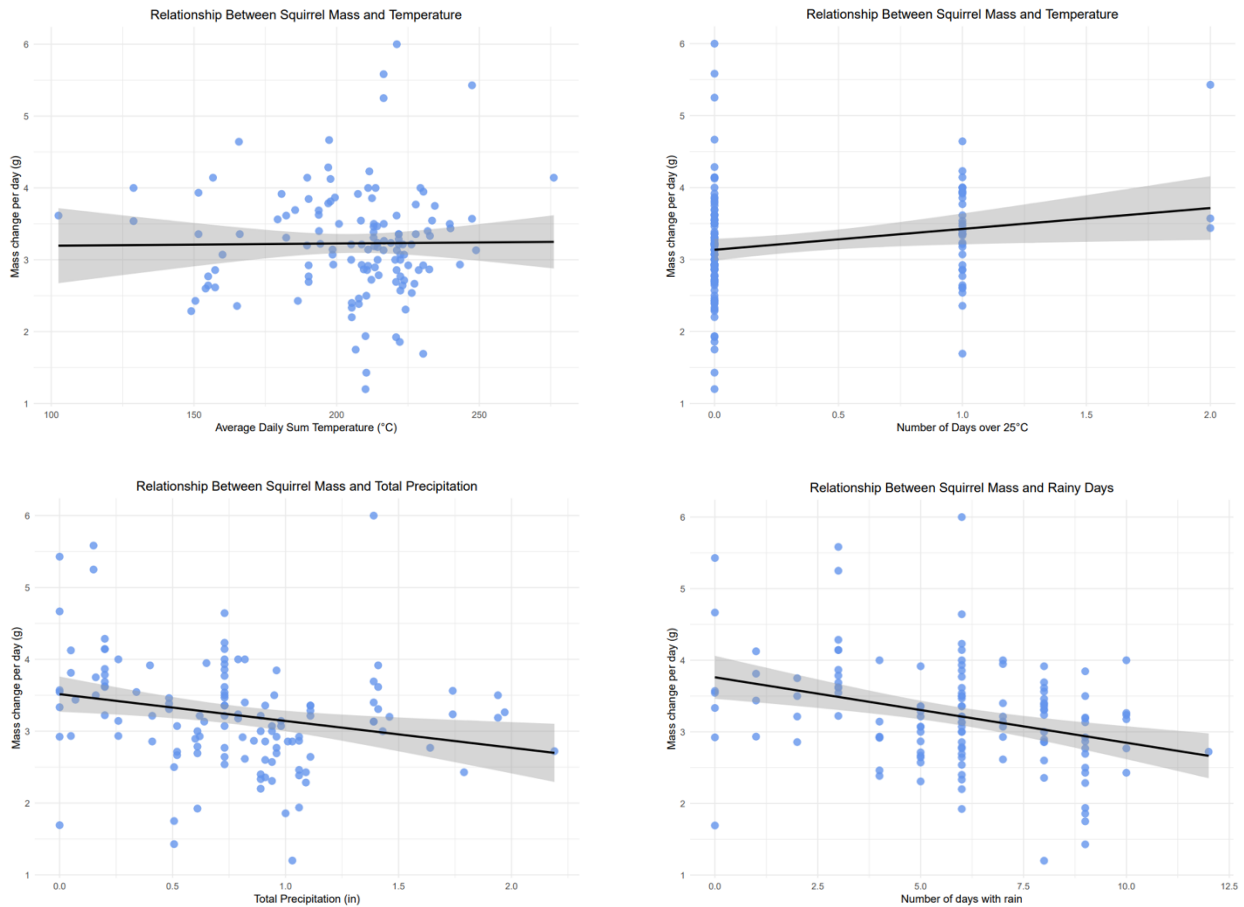


Figure 3. Relationships between mass change, temperature, and precipitation. Top left compares mass change per day with the average daily sum temperature during the growth period. Top right compares mass change per day to the number of days over 25 degrees Celsius during growth period. Bottom left compares mass change per day to total precipitation during growth period. Bottom right compares mass change per day to number of days with rain during growth period.

Discussion

Maternal identity was the strongest predictor of juvenile growth, accounting for around 30% of the variance in mass change. Maternal identity can affect growth rate in three main ways: Burrow location and maternal investment. Where mothers choose to raise their young can directly affect growth rate by determining the available nearby food. Burrows near higher quality or density food sources could increase growth rate in juveniles, both pre and post emergence. Food quality has been found to have a direct effect on body size in other organisms (Smith et al. 2013), so it is possible that nearby food could influence growth in the GMGS. Additionally, moms can also move pups to new locations, and the frequency of this behavior could have positive or negative effects on growth rate based on the locations pups are relocated to. The second way that mom can affect juvenile growth rate is by maternal investment. Though mom does not feed pups much once they've emerged, she can influence their foraging behavior by limiting time spent being vigilant. Mom can alarm call for pups when a threat is near, and if mom is often around and looking out for predators, pups can spend less time vigilant, and thus, more time foraging. Studies on another ground squirrel species, the yellow-bellied marmot (*Marmota flaviventris*), found a strong negative correlation between time spent foraging vs time spent being vigilant (Churma et al. 2016), and an investigation into alarm calling in the Belding's ground squirrel (*Spermophilus beldingi*) found assisting relatives to be the most likely reason for alarm calling (Sherman, 1997). The third way in which maternal identity could affect growth rate is by genetics. Numerous studies have found significant genetic components to body mass, energy acquisition, and growth rates across taxa (e.g. Atchley & Zhu, 1997; Billerbeck, Lankford & Conover, 2001; Laugen et al. 2003), therefore there could be a genetic component to how much a juvenile squirrel is growing.

Our insignificant results on the effects of average temperature and growth rates align with the findings of similar studies on growth rates in mammals. A review paper on the effects of climate on hibernating mammals found only 11 studies describing the effects on body mass and condition, and of those, many had insignificant results (Wells et al. 2022). A few studies, particularly in bats, found positive effects of higher temperatures on body condition, with the explanation that higher temperature could increase food availability (e.g. insects) (Zahn et al. 2007). The relationship between temperature and growth rates in GMGS could be in part explained similarly, as higher temperatures can increase plant growth and flowering (Jagadish et al. 2016), which in turn increases food availability. This could explain why more days with temperatures exceeding 25 degrees Celsius could be beneficial to ground squirrel growth rates, even though pups were seen above ground and foraging less as higher temperatures, as it could mean more available calories to consume when they do forage. However, prolonged high temperatures could be limiting to growth, as an overall higher daily average over the growth period can decrease time spent above ground and foraging. This is supported by the behavioral data, which showed a negative relationship between temperature and foraging behavior.

The relationship between precipitation and growth rate could be explained by the effects of rain on foraging ability. Ground squirrels regularly retreat underground during periods of rain, so if there are numerous rainy days during the growth period, growth rates could decrease as a response to less time spent foraging. Previous research in GMGS found that rainfall had a negative influence on juvenile survival (Kneip et al. 2011), with the same rationale that rain limits access to food. The lack of a significant relationship between total precipitation during the growth period and growth rate is likely because total precipitation does not describe how often it rains, yet the negative effects of rain on growth rate are more due to the frequency of rain, rather than the net amount.

Further directions for this study would be to continue exploring variables affecting growth rates in juveniles. Because of the strength of the impact maternal identity has on pup growth rates, the mechanism and reasons behind that relationship should be explored. The role of burrow location or maternal presence and alarm calling after emergence on growth rate could be assessed. Additionally, there could be a genetic component to growth rate, which could be investigated by comparing maternal growth rates to her pups. The factors contributing to the variation in growth rate per year could also be explored, such as assessing plant composition or density. A study determining at what temperature juveniles must expend more energy thermoregulating than gained from foraging could help explain at what point temperature affects foraging behavior and mass gain. Because of the large variation in juvenile growth rates and the importance of mass gain for juvenile overwinter survival, it is important to continue to explore what factors influence mass gain, for ground squirrels and other hibernating mammals.

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