Impact of Litter Emergence Timing on Pup Growth Rate of Golden-Mantled Ground Squirrels

Marcella Willett
Mentors: Dr. Caitlin Wells and Travis Rainey
Full-Time Independent Research - 2026

Abstract

Phenological mismatch has been shown to impact juvenile growth and body condition in several species of birds, but its effects on juvenile growth in small mammals are less well-documented. Golden-mantled ground squirrels (Callospermophilus lateralis, GMGS) are a small, hibernating mammal to whom body mass is particularly important for survival during their first winter. Using historic data from 1996-2021 from long-term studies at the Rocky Mountain Biological Laboratory, I investigated how GMGS pup growth rate is affected by litter emergence timing relative to the timing of peak abundance of common dandelions (Taraxacum officinale), a key diet item for GMGS. I found that pups emerging slightly later relative to peak dandelion abundance (greater mismatch) showed lower growth rates within two-weeks of emergence, with weaker effects of emergence timing on four and six-week growth rates, suggesting that older pups are better able to buffer against the effects of mismatch.

Introduction

Anthropogenic climate change can have profound effects on the phenology (timing of life history events) of many species. Globally, spring life history events have shifted earlier by an average of 2.3 days per decade (Parmesan & Yohe, 2003). However, these phenological shifts are not consistent across species. Even within the same ecosystem, many species respond to different cues (eg. snowmelt or temperature) or respond in different ways to the same cues (Prather et al., 2023). For instance, climatic changes tend to have greater effects on species in lower trophic levels than those in higher trophic levels (Thackeray et al., 2016). This has the potential to lead to phenological mismatches, where the timing of resource abundance and consumer demand do not align, which can lead to negative effects on fitness (Plard et al., 2014; Visser & Phillip, 2019).

The majority of research on the impacts of climate on phenology has focused on birds, insects, agriculture, or marine systems (Hickinbotham et al., 2025). A recent review of climate change impacts on hibernating mammals found only 17 articles investigating phenological consequences (Wells et al., 2022). Many hibernating mammals live in mountain regions, making them particularly susceptible to the effects of climate change, as their potential for range shifts is restricted, and as mountain regions tend to experience greater warming than nearby lower elevation sites (Geiser, 2013; Pepin et al., 2022). Studies of hibernating mammals have generally found earlier shifts in spring phenology or no effect of climatic changes (Wells et al., 2022). Climactic shifts have also generally been associated with increasing reproductive success in hibernating mammals but have had mixed effects on body condition and survival, with impacts on body mass and condition being particularly understudied (Wells et al., 2022).

Golden mantled ground squirrels (*Callospermophilus lateralis*; GMGS) are small, diurnal mammals that hibernate over winter. Female GMGS give birth in underground burrows to 1-8 pups (Kneip et al., 2011, Wells & Vuren, 2025), which remain underground until weaning at around 30 days old (Phillips, 1981; Wells & Vuren, 2025). A long-term study of GMGS has been conducted at the Rocky Mountain Biological Laboratory (RMBL) since 1990 Wells & Vuren, 2025). GMGS at RMBL show a short active season of around 4 months in which they must raise litters and gain mass for hibernation, making them a particularly interesting system to

study the phenology of. The date of snowmelt at RMBL has been advancing by an average of 2.4 days per decade since 1975 (Prather et al., 2023). GMGS have closely tracked this change, with litter emergence advancing by an average of 2.3 days per decade (Wells & Vuren, 2025). However, the time between snowmelt and litter emergence decreases with earlier snowmelt dates (Wells & Vuren, 2025). Because vegetation phenology typically closely tracks snowmelt (Prather et al., 2023), this indicates that litters are likely emerging later relative to vegetative phenology as snowmelt date becomes earlier.

Importantly for recruitment, female survival and reproduction as yearlings are positively associated with pre-hibernation body mass (Howland et al., 2024). Later emergence for female GMGS pups has been found to lead to decreased pre-hibernation body mass, likely primarily due to decreased number of days spent foraging (Howland et al., 2024). Another contributing factor may be a decreased growth rate for late-emerging squirrels, as indicated by one study investigating the growth rates of 26 female GMGS pups (Wells & Van Vuren, 2018). Additional analysis has confirmed the negative relationship between emergence date and growth rate, though this may be driven by the impact of maternal age, with litters born to yearling mothers emerging later in the season and showing slower growth rates (Wells, unpublished analysis). However, these findings have not been consistent across analyses with another analysis of pup growth rates found no significant effect of maternal age or emergence timing relative to snowmelt on growth rates (Simmons, 2024). Further research is needed to confirm the relationship between emergence timing and growth rate and its potential causes.

If later emerging pups do show a slower growth rate for later emerging pups, this may be due to decreases in the quality or availability of vegetation for forage over the course of the summer (Wells & Van Vuren, 2018). Natural food availability has been shown to impact the growth rate of young in birds (Lepage et al., 1998; Pearce-Higgins & Yalden, 2004; Saalfeld et al., 2019; Schekkerman et al., 2003), but studies on mammals are more limited (Moorhouse et al., 2008). Food supplementation studies have found increased growth rates or no effect on juvenile growth in arctic ground squirrels (*Spermophilus parryii plesius*, Hubbs & Boonstra, 1997; Karels et al., 2000). In water voles (*Arvicola terrestris*), decreased availability of forage per individual (caused by smaller range size) results in longer time to reach maturity, indicating slower growth rates (Moorhouse et al., 2008). In Columbian ground squirrels (*Spermophilus columbianus*), food quality, as indicated by ratio of forbs to grasses or digestibility (forbs are 30-50% more digestible than grasses), is a more important factor in juvenile growth than overall plant biomass (Bennett, 1999).

The phenological match-mismatch hypothesis (i.e., Cushing hypothesis) proposes that a consumer's fitness should be highest when the timing of its most energetically demanding period aligns with the timing of peak resource availability (Cushing, 1969; Kharouba & Wolkovich, 2020). A mismatch can occur if the consumer's peak demand occurs either before or after the peak resource availability, resulting in a unimodal relationship between fitness and the relative timing of the energetically demanding period (Cushing, 1969; Kharouba & Wolkovich, 2020). This unimodal relationship has been observed in the body condition of several species of arctic shorebird chicks depending on their hatch-timing relative to peak insect availability (Lameris et

al., 2021) and in the condition of pied flycatcher (*Ficedula hypoleuca*) chicks, which showed the highest condition if they hatched 8-9 days before peak caterpillar availability (Samplonius et al., 2016).

At RMBL common dandelions (*Taraxacum officinale*) made up 40-90% of the diet of GMGS, which prefer dandelions to other plants when available (Carleton, 1966). If GMGS preference is indicative of food quality, the timing of dandelion abundance may serve as an indicator of the availability of quality forage. The flowering time of dandelions at RMBL has been tracked every year since 1974 (excluding 1978 and 1990) as part of a long-term study on flowering plants (Prather et al., 2023). Previous analysis of GMGS growth rate only included a two-week growth window after emergence and was limited to squirrels born in or after 2018, when regular two-week weight measurements began to be taken (Simmons, 2024). This analysis utilizes data going back to 1996 and looks at multiple temporal scales (two-week, four-week, and six-week) to determine if growth rates are influenced differently across development.

In this paper, I analyze how the timing of litter emergence relative to peak dandelion abundance impacts growth rate and how this relationship is influenced by yearly dandelion abundance. I hypothesize that growth rates will show a unimodal relationship with the difference between emergence date and peak dandelion abundance, with litters emerging further before or after peak dandelion abundance showing slower growth rates. I hypothesize that growth rates will peak with emergence dates slightly before peak dandelion abundance to maximize the time during their growth period in which pups will have access to more of this key diet item. Additionally, I hypothesize that these effects will be stronger in years of lower dandelion abundance, when pups are more likely to be resource limited. Alternatively, if synchrony between dandelion abundance and emergence timing does not affect growth rate, this would suggest that pups are able to buffer against the effects of phenological mismatch, likely through diet switching to other food resources (Weir & Phillimore, 2024).

Methods

This project uses data from the long-term dataset on golden-mantled ground squirrels, collected at RMBL between 1996 and 2021 (Figure 1). GMGS were trapped using Tomahawk Model 201 live traps baited with sunflower seeds and peanut butter. Squirrels were given uniquely numbered Monel fingering eartags (National Band & Tag Company, Newport, KY) and black dye-marks (Nyanzol-D dye) to allow for individual identification and re-sighting from a distance. While captured, squirrels were weighed using a spring-scale accurate to 1 g, anogenital distance was measured to determine sex, and reproductive status was recorded for females based on nipple development.

Figure 1. Map of long-term golden-mantled ground squirrel study site at RMBL.

The home ranges of lactating adult females were searched multiple times per day for pups to determine the date of litter emergence. Precise litter emergence dates (within 24 hours) have been recorded for most litters since 1994 (Wells & Vuren, 2025). Pups were trapped on the emergence day if possible (or within 48 hours), weight and anogenital distance were recorded, and pups were given unique ear tags and a dye mark for individual identification. Pups were recaptured periodically throughout the summer and weight was re-taken. Since 2018, an effort has been made to recapture all pups around 2-weeks after emergence. Maternal identity was tentatively identified based on location of emergence within the home range of a lactating female and confirmed through observations of interactions between the adult female and pups (Ferron, 1985; Wells & Vuren, 2025). Additionally, maternity for pups born 1996-2005 and 2007-2015 was confirmed using multilocus microsatellite genotypes (Wells et al., 2017; Wells & Vuren, 2025).

I extracted data on trap dates and pup weights upon initial capture (up to 2 days after emergence) and in three intervals to measure growth: a 2-week interval (10-19 days), a 4-week interval (24-32 days), and a 6-week interval (38-46 days). If pups were captured multiple times within this interval, I selected the capture closest to the center of the interval (14 days, 28 days, and 42 days). If pups were weighed multiple times on the same day, the average was taken of those weights. Only pups for whom maternal identity, maternal age (yearling or non-yearling), and precise emergence date (within a 4-day window) were known were used in this study. This resulted in 277 observations for the 2-week growth interval, 148 observations for the 4-week growth interval, and 96 observations for the 6-week growth interval. Growth rates were calculated separately for each interval by dividing the change in mass by the number of days since initial capture.

Data on dandelion flowering abundance was extracted from a long-term study of plant flowering timing and abundance at RMBL conducted since 1974. In this study flowers on 2x2

meter plots were counted approximately every other day during the growing season (Prather et al., 2023, supplementary information). For my analysis, I combined the data from the eight rocky meadow plots, five willow-meadow interface plots, and five wet meadow plots (by adding the counts from each plot to create a total count for each date). I fitted a generalized additive model (GAM) to each year separately, predicting dandelion abundance based on date using the restricted maximum likelihood method (REML) with 30 knots. Peak dandelion count was calculated as the maximum prediction of the GAM with peak flowering date being the corresponding day of year. Relative emergence date was measured as the difference in days between emergence date and peak flowering date (with negative values indicating an emergence before peak flowering time). Additionally, to account for differences in the steepness of flower abundance peaks across years, relative emergence date was multiplied by a rescaling factor of the difference between the yearly peak flowering abundance and the mean flowering abundance during the growth period of each pup (calculated separately for the two, four, and six-week intervals), following the methods of Lameris et al., 2021. For example a pup emerging 3 days after the date of peak dandelion abundance and experiencing an average dandelion availability of 4.6 dandelions/day over the four week period (compared to a peak dandelion count of 21.4) would have a rescaled relative emergence of 50.4 (3 x (21.4 - 4.6)).

The relationship between relative emergence date and growth rate was modeled separately for each of the three growth periods using generalized linear mixed-effect models (GLMMs) in *lme4* (Bates et al., 2026). For each growth period, I fitted two global models using either relative emergence date or rescaled relative emergence as a predictor. Since a unimodal relationship was expected the term of relative emergence or rescaled relative emergence squared was also included in the model (Lameris et al. 2021). Additional fixed effects included in the models were pup sex, initial mass at emergence, and age of mother (yearling or post-yearling) with random effects of year and mother identity. For the relative emergence models, I included predictors of peak dandelion count and the interactions between peak count and relative emergence as well as peak count and relative emergence squared. Peak count was highly correlated with rescaled relative emergence (as it was used to calculate that term), so it was not included in models of rescaled relative emergence. Initial mass at emergence, minimum litter size, and peak dandelion count were all centered before use in the models to aid in ease of interpretation.

Additionally, piecewise models of the effects of relative emergence or rescaled relative emergence on growth rate were also tested to determine if effects were threshold-dependent. Models of rescaled and non-rescaled relative emergence were with the same additional predictors excluding interactions (peak count also had to be excluded in the four-week relative emergence model due to failure to converge). Integer breakpoints were tested over the entire range of rescaled and non-rescaled relative emergence for each model, with models of different breakpoints being compared using AIC values.

Results

There was considerable variation in growth rates, ranging between 1.2 and 6 grams per day (Table 1). Growth rates tended to be slightly lower as the time interval increased (two weeks vs four weeks vs. six weeks). Emergence dates also varied significantly, between 7 days before peak dandelion abundance and 51 days after peak dandelion abundance. However, there were only 10 total pups that emerged before peak dandelion date (10 with two-week measurements, 5 with four-week, and 1 with six-week), with all but one pup being from two litters in 2019. The range of late-season emergences was slightly more limited for the longer intervals with the latest emergence date being 36 days after peak dandelion abundance for the six-week interval, 46 for the four-week interval, and 51 for the two-week intervals.

Table 1. Summary statistics. Continuous variables expressed as mean (range).

Variables	Two-week (n = 277)	Four-week (n = 148)	Six-week (n = 96)
Growth rate (g/day)	3.202 (1.2, 6)	3.000 (1.414, 4.355)	2.870 (1.282, 4.045)
Relative emergence (days)	23.91 (-7, 51)	23.94 (-7, 46)	23.4 (-2, 36)
Rescaled relative emergence	873.3 (-112.4, 2931.9)	697.9 (-161.6, 2937.6)	671.59 (-28.95, 2420.57)
Minimum litter size	5.264 (1, 8)	5.068 (1, 7)	5.229 (2, 8)
Initial capture weight (g)	74.93 (46, 120)	75.32 (48, 113)	73.96 (47, 117)
Males:Females	115:162	60:88	30:66
Yearling:Non-yearling mother	73:204	41:107	32:64

Two-week growth rates

There was moderate evidence of a negative relationship between relative emergence and two-week growth rate, with pups growth rate decreasing by 0.047 ± 0.015 grams per day as emergence date moved one day later relative to peak dandelion abundance (t = -3.069). However, there was only moderately weak evidence of a relationship between relative emergence squared and two-week growth rate (0.00070 ± 0.00036, t = 1.949). Together, these two terms demonstrate a decreasing rate of decline in growth rates as relative emergence increases with a slight increase in growth rates for relative emergences 34 days after peak dandelion abundance (Figure 2a). Additionally, contrary to my hypotheses, peak dandelion abundance showed very little evidence of a negative relationship with growth rates (-0.013 ± 0.012, t = -1.111), and the interactions between abundance and relative emergence did not show any evidence of a relationship with growth rate (Relative Emergence*Peak: 0.00067 ± 0.0011, t = 0.609; Relative Emergence^2*Peak: 0.0000032 ± 0.000025, t = -0.130). Another predictor that showed moderate evidence of a relationship with two-week growth rate was initial mass at emergence, with larger pups at emergence showing slower two-week growth rates (-0.0093 ± 0.0037, t = -2.474). There was no evidence of relationship for minimum litter size (0.021 ±

0.041, t = 0.520) and sex (Male: 0.048 ± 0.079, t = 0.610), and very little evidence of a negative effect of the mother being a yearling (-0.15 ± 0.13, t = -1.104). The random effect of mother identity explained a larger percentage of the variance than the random effect of year (36.3% vs 7.2%). Tests of piecewise models showed the lowest AIC for a breakpoint at the minimum relative emergence, suggesting a piecewise relationship was not supported.

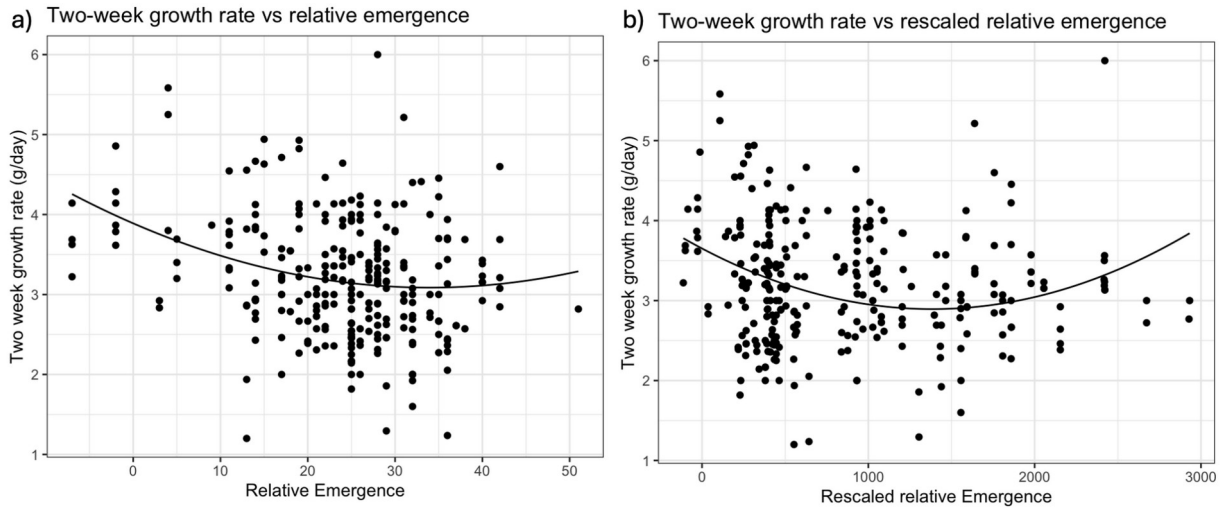

Figure 2. Relative emergence (days between peak dandelion abundance and litter emergence, a) and rescaled relative emergence (see methods, b) plotted against two-week growth rate. Curves are generated from the slopes of rescaled and non-rescaled relative emergence and rescaled and non-rescaled relative emergence squared as well as the intercepts from those models.

When relative emergence was rescaled to account for differences in the steepness of peak dandelion abundance, both rescaled relative emergence and rescaled relative emergence squared showed strong evidence of relationships with two-week growth rate (Rescaled emergence: -0.0011 ± 0.0003, t = -3.598, $4.0 \times 10^{-7} \pm 1.2 \times 10^{-7}$, t = 3.270). Pups emerging later relative to peak abundance and experiencing a greater difference between dandelion availability during their growth period and peak dandelion availability showed slower growth rates initially. However, the slope of this relationship became more shallow and eventually switched to increasing growth rates with rescaled emergences greater than 1375 (Figure 2b). Additionally, initial weight at capture showed strong evidence of a relationship with growth rate with pups 1 gram larger showing growth rates 0.012 ± 0.0037 grams/day lower (t = -3.183). There was still no evidence of a relationship for minimum litter size (-0.024 ± 0.042, t = -0.578) and sex (Male: 0.058 ± 0.077, t = 0.754) and very weak evidence of an effect of having a yearling mother (-0.19 ± 0.13, t = -1.456). The random effect of mother identity continued to explain a larger percentage of the variance than the random effect of year (38.2% vs 12.5%). Tests of piecewise models showed the lowest AIC for a breakpoint at the minimum rescaled relative emergence, suggesting a piecewise relationship was not supported.

Four-week growth rates

In the four-week growth rate models, relative emergence showed very little evidence of a negative relationship with growth rate (-0.019 ± 0.017, t = -1.116, Figure 3a) and relative emergence squared showed no evidence of a relationship (-0.00035 ± 0.00039, t =0.899). Like the two-week model, there was very strong evidence of an effect of initial weight at emergence, with pups 1 gram larger showing slower growth rates by an average of 0.016 ± 0.0043 grams/day (t = -3.607). Additionally, pup sex emerged as having moderate evidence of a relationship with growth rate with male pups showing a growth rate higher by 0.17 ± 0.069 grams/day (t = 2.411). There was very little evidence of positive relationships with growth rate for minimum litter size (0.050 ± 0.040, t = 1.245) and peak dandelion count (0.015 ± 0.12, t = 1.220). The interactions between peak dandelion abundance and relative emergence showed very little evidence of relationships (Relative Emergence*Peak: -0.0016 ± 0.0012, t = -1.354; Relative Emergence^2*Peak: 0.000044 ± 0.000027, t = 1.648). Additionally, there was no evidence of a relationship between having a yearling mother and growth rate (-0.12 ± 0.13, t = -0.950). Like the two week models, mother identity explained a larger percentage of the variance than year (37.3% vs 23.3%). Additionally, a piecewise model was tested (excluding peak count as a predictor due to failure to converge), but the breakpoint with the lowest AIC remained the minimum data point, suggesting relative emergence does not show a threshold-based effect.

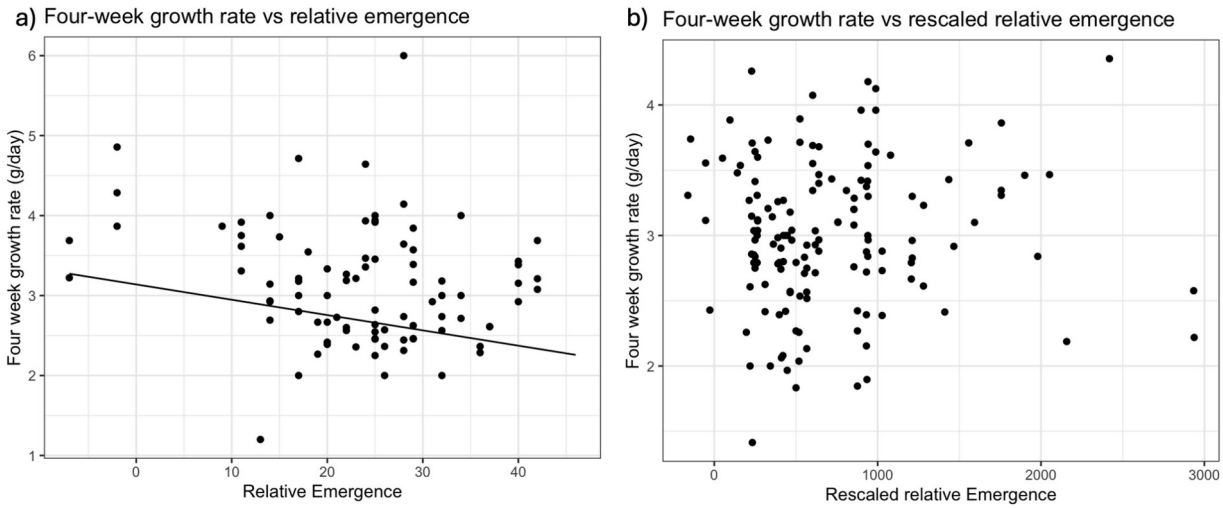

Figure 3. Relative emergence (days between peak dandelion abundance and litter emergence, a) and rescaled relative emergence (see methods, b) plotted against four-week growth rate. The line in graph (a) is generated from the slope of relative emergence and the intercept of the model. Relative emergence squared and the rescaled relative emergence curve were not plotted because there was no evidence of a relationship.

The model using rescaled relative emergence to predict four-week growth rate showed very similar results to the model using non-rescaled emergence dates, with emergence timing remaining continuing to show no evidence of a relationship with growth rates (Rescaled

emergence: 0.0000045 ± 0.00027, t = -0.017; Rescaled emergence^2: $5.2x10^{-8}$ ± $1.1x10^{-7}$, t = 0.491; Figure 3b). Initial capture weight and pup sex (male) showed the same relationships with growth rate as in the preceding model with coefficients of -0.015 ± 0.0043 (t = -3.491) and 0.16 ± 0.069 (t = 2.277) grams/day, respectively. Like in the previous model, minimum litter size showed very little evidence of a positive relationship with growth rates (0.058 ± 0.041, t = 1.410). Additionally, there was very little evidence that having a yearling mother was associated with lower growth rates (-0.013 ± 0.012, t = -1.028). Mother identity continued to explain a larger percentage of the variance than year (45.8% vs 14.7%). A test of piecewise models showed the lowest AIC with a breakpoint between a rescaled relative emergence of -52 and -28, which would only separate four data points from the remaining data, not providing enough data to assess potential differences in the relationship.

Six-week growth rates

Similarly to the four-week growth rate models, relative emergence and relative emergence squared showed very little evidence of a relationship with six-week growth rate, with relative emergence showing a possible positive relationship and relative emergence squared showing a possible negative relationship, producing an n-shaped curve (Relative Emergence: 0.047 ± 0.032, t = 1.467; Relative Emergence^2: -0.0010 ± 0.00077, t = -1.317; Figure 4a). Initial capture weight only showed weak evidence of a negative relationship with growth rate in the six-week model (-0.0095 ± 0.0050, t = -1.889), but instead, whether or not the pup's mother was a yearling emerged as a having very strong evidence of a relationship with growth rates, with pups with yearling mothers showing higher growth rates by an average of 0.60 ± 0.11 grams/day (t = 3.965). Sex showed moderately weak evidence of a relationship with growth rate, with male pups growing 0.21 ± 0.11 g/day faster (t = 1.974). There was no evidence of a relationship for minimum litter size (-0.018 ± 0.046, t = -0.398) or for peak dandelion count (0.0053 ± 0.023, t = 0.232) or its interactions (Relative Emergence*Peak: 0.000077 ± 0.0021, t = 0.036; Relative Emergence^2*Peak: -0.000011 ± 0.000048, t = -0.233). Like all previous models, mother identity explained a greater percentage of the variance than year (32.0% vs 6.0%).

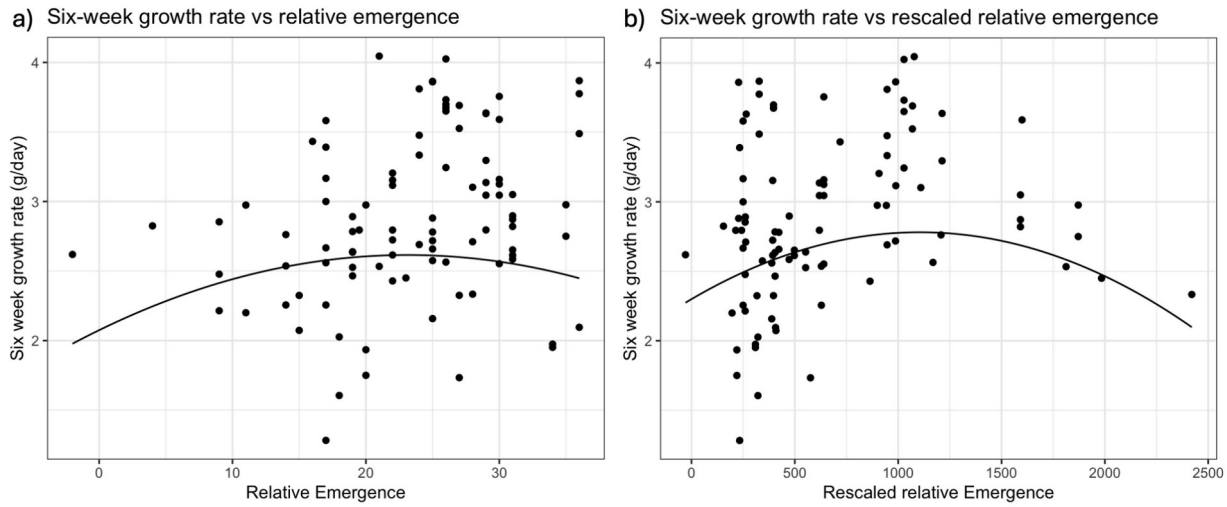

Figure 4. Relative emergence (days between peak dandelion abundance and litter emergence, a) and rescaled relative emergence (see methods, b) plotted against six-week growth rate. Curves are generated from the slopes of rescaled and non-rescaled relative emergence and rescaled and non-rescaled relative emergence squared as well as the intercepts from those models.

There was moderately weak evidence of a positive relationship between rescaled relative emergence and growth rates (0.00087 ± 0.00045, t = 1.949), and moderately weak evidence of a negative relationship between rescaled relative emergence squared and growth rates (-3.9×10^{-7} ± 2.0×10^{-7}, t = -1.944). This produced an overall downward facing parabola where growth rates initially increased with larger rescaled relative emergence and did not begin decreasing until after a rescaled relative emergence of 1115 (Figure 4b). Mother age continued to show strong evidence of a positive relationship with growth rate with pups born to yearling mothers showing higher growth rates by an average of 0.49 ± 0.14 grams/day (t = 3.468). Like the six-week non-rescaled relative emergence model, male pups showed moderately weak evidence of having a faster growth rate (0.21 ± 0.10, t = 1.967). Initial weight continued to show weak evidence of a negative relationship with growth rate (-0.0080 ± 0.0047, t = -1.720), and there remained no evidence of a relationship between minimum litter size and growth rate (-0.0062 ± 0.043, t = -0.143). Mother identity continued to explain a larger percentage of the variance than year (24.5% vs. 5.8%).

A test of piecewise models with different breakpoints on six-week rescaled relative emergence showed the lowest AIC for a model with a breakpoint at a rescaled relative emergence between 630 and 641, separating the data into 58 observations before the breakpoint and 38 after. The earlier rescaled relative emergence interval (<630) showed very strong evidence of a negative relationship with growth rate (-0.0015 ± 0.00044, t = -3.319), while the later rescaled relative emergence showed very weak evidence of a negative relationship with growth rate (-0.00021 ± 0.00014, t = -1.493), suggesting that larger rescaled relative emergences initially affect growth rate but that after a threshold, the effects level out. Like the quadratic model, sex and yearling mother continued to show strong evidence of relationship with growth

rate (Sex Male: 0.26 ± 0.099, t = 2.6478; Yearling Mother: 0.54 ± 0.13, t = 4.181), initial capture showed very weak evidence of a negative relationship (-0.0062 ± 0.0046, t = -1.355), and minimum litter size showed no evidence of a relationship (0.016 ± 0.040, t = 0.410). In this model, mother identity explained 36.8% of the variance while year did not explain any of the variance.

Discussion

As hypothesized, pups emerging later relative to peak dandelion abundance and experiencing a greater difference in dandelion availability from the peak initially showed slower two-week growth rates. This suggests that dandelions are an important diet item during this developmental period or that the timing of dandelion abundance is associated with the abundance of other key diet items during this growth period. However, contrary to my hypothesis, there was little evidence of an impact of relative emergence on growth rates in the four-week and six-week time intervals. This may imply that pups are most resource-limited during the two-week growth period. During this period, pups are first learning to forage, so an abundance of high-quality food may be more important in this time compared to once they have become more experienced foragers. Additionally, pups typically move farther away from their natal burrow as they get older (Nguyen et al., 2025), which indicates that during the four and six-week intervals the pups would be foraging over a larger area, potentially mitigating the effects of having a lower density of dandelions available.

Squirrels consume a variety of different food items and will readily switch to other food sources when dandelions are not highly available (Carleton, 1966). This generalism and resource switching can help to buffer the squirrels against negative effects of mismatch with any one particular resource (Weir & Phillimore, 2024). Because this buffering was more apparent at the four and six week levels than the two-week level, this suggests that older pups may show more generalism or greater flexibility in their food consumption. Additionally, at the population level, the wide range of variation in emergence dates could create a portfolio effect that buffers the population against the potential for phenological mismatch (Weir & Phillimore, 2024).

Dandelions are an introduced species in Colorado (though they have been established at RMBL since at least 1966; Carleton, 1966) and are not found in the same abundance in all regions of the golden-mantled ground squirrel's habitat (Carleton, 1966). In regions where dandelions are less abundant, squirrels consume a variety of seeds, insects, and herbaceous vegetation (Carleton, 1966). The wider variety in diet exhibited by squirrels in other regions may make the results of this study less applicable by creating greater potential for buffering.

The hypothesized relationship of a unimodal curve with a peak when relative emergence is slightly before peak dandelion abundance was not observed. This is likely due to the very low number of litters emerging before peak dandelion availability. Additionally, none of the litters emerged more than 7 days before peak dandelion abundance, meaning that the timing of the peak would still overlap with the measured two-week (and longer) growth interval. This makes it unlikely that we would be able to observe the expected decline in growth rates for litters emerging too early. The upwards curve at later rescaled relative emergences in the two-week

model may be due in part to the decreased number of data points at higher rescaled relative emergences. Additionally, the increased availability of other food resources later in the season such as grass seeds, which also make up part of the squirrels' diet (Carleton, 1966), could underlie increased growth rates.

Though there was only moderately weak evidence of a relationship between emergence timing (rescaled and non-rescaled) and growth rates in the six week interval, the relationship observed was not as hypothesized, with peak growth rates occurring with emergence timings far after peak dandelion abundance. This model may be influenced by the restricted range of emergence dates of litters included in the six-week interval (due to sampling constraints). The later peak could also be influenced by the availability of other food resources. Additionally, golden-mantled ground squirrels mainly consume the stems of dandelions (Carleton, 1966) which remain available after dandelions are done flowering (dandelions take around 14 days after flower closure before they fruit; Collier & Rogstad, 2004). This could potentially lead to a delay where peak growth rates occur with emergences after peak flowering time; although, it is unclear why this would be acting at the six-week level but not the two or four-week levels.

Pups with higher initial capture weights show slower growth rates in both the two-week and four-week intervals. This is likely compensatory growth, suggesting that smaller emerging pups are able to, at least in part, make up for their smaller initial mass by growing at a faster rate. Post-weaning compensatory growth for initially smaller individuals has been observed in northern grasshopper mice (*Onychomys leucogaster*), bank voles (*Clethrionomys glareolus*), red squirrels (*Tamiasciurus hudsonicus*), and prairie voles (*Microtus ochrogaster;* Kerr, 2006; Oksanen et al., 2002; Sikes, 1998; Solomon, 1994) but not alpine marmots (*Marmota marmota*; Allainé et al., 1998), although the observed compensatory growth is not always enough to fully catch up to their initially heavier counterparts (Solomon, 1994). In GMGS, compensatory growth is no longer apparent in the six-week growth interval, perhaps because the influences of individual and environmental variation over the longer time period dilute the effects of compensating for a smaller initial mass.

Interestingly, sex-related differences in growth rate are only apparent in the four-week (and to a lesser extent the six-week) growth interval. In golden-mantled ground squirrels, male and female pups do not show significant differences in emergence mass (Wells & Van Vuren, 2017), although they do show slight sexual mass dimorphism later in life with males having lower adult body masses but also reaching adult body mass sooner (Howland et al., 2024). The higher growth rates observed for male pups in the four and six-week intervals may be because GMGS exhibit male-biased dispersal (Nguyen et al., 2025), so it may be necessary for males to gain a higher body mass in order to prepare for dispersal. This relationship is slightly weakened in the six-week interval, which may occur because the faster-growing male pups will already have begun to disperse by that time, leaving the males with growth rates closer to those of the females. Faster growth rates in male pups have also been observed in arctic ground squirrels (*Urocitellus parryii*, (Wheeler & Hik, 2014), which also show male-biased dispersal (Byrom & Krebs, 1999). In the arctic ground squirrels, the faster growth rate for male pups also lead to

higher pre-hibernation masses (Wheeler & Hik, 2014), although it is unclear if this would be true for golden-mantled ground squirrels.

Mother age (yearling or non-yearling) only had a significant effect on pup growth rate in the six-week model with yearling mothers showing faster growing pups. There is limited research on maternal effects on offspring post-weaning, with most studies focussing on offspring during lactation and finding faster growth rates in offspring from older or middle-aged mothers (Bowen et al., 2001; Parra Faundes, 2015; Rödel et al., 2008). Similarly, a study on post-weaning growth in mountain goats (*Oreamnos americanus*), found higher body masses for yearling males with older mothers but no effect on masses of yearling females or second-years of either sex (Gendreau et al., 2005). Post-weaning survival and lifetime reproductive success have also been found to be higher for offspring born to older or middle-aged mothers (Meijer et al., 2011; Rödel et al., 2009), though in one species this is due to lower mortality from predators rather than differences in body condition (Meijer et al., 2011). The opposite effect on growth rates observed in golden-mantled ground squirrels may be due to behavioral differences between yearling and adult mothers. Potentially yearling mothers remain vigilant around their pups aboveground for a longer period of time (after older mothers have already immerged for hibernation underground), allowing the pups more time to devote to foraging during the six-week interval.

Overall, my results demonstrate that phenological mismatch with dandelion resources is most likely to affect golden-mantled ground squirrel pups in their early post-weaning development and that older pups are better able to buffer against the effects of mismatch. These results suggest that if climate change causes increased mismatch between GMGS emergence timing and dandelion availability, pups will likely be able to mostly avoid long-term effects on their growth, unless mismatch advances far beyond the levels observed in this study. Future research could investigate differences in diet and foraging behavior as pups age to determine the mechanisms older pups are using to buffer against mismatch.

References

Allainé, D., Graziani, L., & Coulon, J. (1998). Postweaning mass gain in juvenile alpine marmots Marmota marmota. *Oecologia*, *113*(3), 370–376. https://doi.org/10.1007/s004420050388

Bates, D., Maechler, M., Bolker, B., Walker, S., Ly, A., Jagan, M., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., Pavel, N. K., Tanaka, E., Boylan, R. D., & Bengtsson, H. (2026). *lme4: Linear Mixed-Effects Models using "Eigen" and S4* (Version 2.0-6) [Computer software]. https://cran.r-project.org/web/packages/lme4/index.html

Bennett, R. P. (1999). Effects of food quality on growth and survival of juvenile Columbian ground squirrels (Spermophilus columbianus). *Canadian Journal of Zoology*, *77*(10), 1555–1561. https://doi.org/10.1139/z99-144

Bowen, W. D., Ellis, S. L., Iverson, S. J., & Boness, D. J. (2001). Maternal effects on offspring growth rate and weaning mass in harbour seals. *Canadian Journal of Zoology*, *79*(6), 1088–1101. https://doi.org/10.1139/z01-075

Byrom, A. E., & Krebs, C. J. (1999). Natal dispersal of juvenile arctic ground squirrels in the boreal forest. *Canadian Journal of Zoology*, *77*(7), 1048–1059. https://doi.org/10.1139/z99-072

Carleton, W. M. (1966). Food Habits of Two Sympatric Colorado Sciurids. *Journal of Mammalogy*, *47*(1), 91–103. https://doi.org/10.2307/1378073

Collier, M. H., & Rogstad, S. H. (2004). Clonal variation in floral stage timing in the common dandelion Taraxacum officinale (Asteraceae). *American Journal of Botany*, *91*(11), 1828–1833. https://doi.org/10.3732/ajb.91.11.1828

Cushing, D. H. (1969). The Regularity of the Spawning Season of Some Fishes. *Journal Du Conseil*, *33*(1), 81–92. https://doi.org/10.1093/icesjms/33.1.81

Ferron, J. (1985). Social behaviour of the golden-mantled ground squirrel (Spermophilus lateralis). *Canadian Journal of Zoology*, *63*(11), 2529–2533. https://doi.org/10.1139/z85-375

Geiser, F. (2013). Hibernation. *Current Biology*, *23*(5), R188–R193. https://doi.org/10.1016/j.cub.2013.01.062

Gendreau, Y., Côté, S. D., & Festa-Bianchet, M. (2005). Maternal effects on post-weaning physical and social development in juvenile mountain goats (Oreamnos americanus). *Behavioral Ecology and Sociobiology*, *58*(3), 237–246. https://doi.org/10.1007/s00265-005-0938-2

Grimland, E. (2024). Effects of trophic phenological synchrony or dyssynchrony on maternal investment of a small herbivorous mammal (Callospermophilus lateralis). *RMBL Student Papers*.

Hickinbotham, E. J., Ridley, F. A., Rushton, S. P., & Pattison, Z. (2025). 30 years of climate related phenological research: Themes and trends. *International Journal of Biometeorology*, *69*(6), 1459–1473. https://doi.org/10.1007/s00484-025-02903-w

Howland, S., Wells, C. P., & Van Vuren, D. H. (2024). Causes and consequences of pre-hibernation body mass in golden-mantled ground squirrels (Callospermophilus lateralis). *Journal of Mammalogy*, *105*(2), 348–357. https://doi.org/10.1093/jmammal/gyad131

Hubbs, A. H., & Boonstra, R. (1997). Population Limitation in Arctic Ground Squirrels: Effects of Food and Predation. *Journal of Animal Ecology*, *66*(4), 527–541. https://doi.org/10.2307/5947

Karels, T. J., Byrom, A. E., Boonstra, R., & Krebs, C. J. (2000). The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. *Journal of Animal Ecology*, *69*(2), 235–247. https://doi.org/10.1046/j.1365-2656.2000.00387.x

Kharouba, H. M., & Wolkovich, E. M. (2020). Disconnects between ecological theory and data in phenological mismatch research. *Nature Climate Change*, *10*(5), 406–415. https://doi.org/10.1038/s41558-020-0752-x

Kneip, É., Van Vuren, D. H., Hostetler, J. A., & Oli, M. K. (2011). Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels. *Journal of Mammalogy*, *92*(2), 367–377. https://doi.org/10.1644/10-MAMM-A-156.1

Lameris, T. K., Tomkovich, P. S., Johnson, J. A., Morrison, R. I. G., Tulp, I., Lisovski, S., DeCicco, L., Dementyev, M., Gill Jr., R. E., ten Horn, J., Piersma, T., Pohlen, Z., Schekkerman, H., Soloviev, M., Syroechkovsky, E. E., Zhemchuzhnikov, M. K., & van Gils, J. A. (2022). Mismatch-induced growth reductions in a clade of Arctic-breeding shorebirds are rarely mitigated by increasing temperatures. *Global Change Biology*, *28*(3), 829–847. https://doi.org/10.1111/gcb.16025

Lepage, D., Gauthier, G., & Reed, A. (1998). Seasonal Variation in Growth of Greater Snow Goose Goslings: The Role of Food Supply. *Oecologia*, *114*(2), 226–235.

Meijer, T., Norén, K., & Angerbjörn, A. (2011). The impact of maternal experience on post-weaning survival in an endangered arctic fox population. *European Journal of Wildlife Research*, *57*(3), 549–553. https://doi.org/10.1007/s10344-010-0463-0

Moorhouse, T. P., Gelling, M., & Macdonald, D. W. (2008). Effects of Forage Availability on Growth and Maturation Rates in Water Voles. *Journal of Animal Ecology*, *77*(6), 1288–1295.

Nguyen, N. T. T., Wells, C. P., & Van Vuren, D. H. (2025). Dispersal of the Golden-mantled Ground Squirrel (Callospermophilus lateralis). *Journal of Mammalogy*, *106*(2), 313–322. https://doi.org/10.1093/jmammal/gyae106

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Parra Faundes, D. (2015). *Sex allocation, terminal investment and the effects of environmental constraints on maternal investment in subtropical antechinus* [PhD Thesis, The University of Queensland]. https://doi.org/10.14264/uql.2015.380

Pearce-Higgins, J. W., & Yalden, D. W. (2004). Habitat selection, diet, arthropod availability and growth of a moorland wader: The ecology of European Golden Plover Pluvialis apricaria chicks. *Ibis*, *146*(2), 335–346. https://doi.org/10.1111/j.1474-919X.2004.00278.x

Pepin, N. C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., Palazzi, E., Seibert, P., Serafin, S., Schöner, W., Terzago, S., Thornton, J. M., Vuille, M., & Adler, C. (2022). Climate Changes and Their Elevational Patterns in the Mountains of the World. *Reviews of Geophysics*, *60*(1), e2020RG000730. https://doi.org/10.1029/2020RG000730

Phillips, J. A. (1981). Growth and its relationship to the initial annual cycle of the golden-mantled ground squirrel, Spermophilus lateralis. *Canadian Journal of Zoology*, *59*(6), 865–871. https://doi.org/10.1139/z81-124

Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A. J. M., Delorme, D., Warnant, C., & Bonenfant, C. (2014). Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. *PLOS Biology*, *12*(4), e1001828. https://doi.org/10.1371/journal.pbio.1001828

Prather, R. M., Dalton, R. M., barr, billy, Blumstein, D. T., Boggs, C. L., Brody, A. K., Inouye, D. W., Irwin, R. E., Martin, J. G. A., Smith, R. J., Van Vuren, D. H., Wells, C. P., Whiteman, H. H., Inouye, B. D., & Underwood, N. (2023). Current and lagged climate affects phenology across diverse taxonomic groups. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1990), 20222181. https://doi.org/10.1098/rspb.2022.2181

Rödel, H. G., Prager, G., Stefanski, V., von Holst, D., & Hudson, R. (2008). Separating maternal and litter-size effects on early postnatal growth in two species of altricial small mammals. *Physiology & Behavior*, *93*(4), 826–834. https://doi.org/10.1016/j.physbeh.2007.11.047

Rödel, H. G., Von Holst, D., & Kraus, C. (2009). Family legacies: Short- and long-term fitness consequences of early-life conditions in female European rabbits. *Journal of Animal Ecology*, *78*(4), 789–797. https://doi.org/10.1111/j.1365-2656.2009.01537.x

Saalfeld, S. T., McEwen, D. C., Kesler, D. C., Butler, M. G., Cunningham, J. A., Doll, A. C., English, W. B., Gerik, D. E., Grond, K., Herzog, P., Hill, B. L., Lagassé, B. J., & Lanctot, R. B. (2019). Phenological mismatch in Arctic-breeding shorebirds: Impact of snowmelt and unpredictable weather conditions on food availability and chick growth. *Ecology and Evolution*, *9*(11), 6693–6707. https://doi.org/10.1002/ece3.5248

Samplonius, J. M., Kappers, E. F., Brands, S., & Both, C. (2016). Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine. *Journal of Animal Ecology*, *85*(5), 1255–1264.

Schekkerman, H., Tulp, I., Piersma, T., & Visser, G. H. (2003). Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. *Oecologia*, *134*(3), 332–342. https://doi.org/10.1007/s00442-002-1124-0

Simmons, K. (2024). Investigating the role of climate on juvenile Golden-mantled ground squirrel (Callospermophilus lateralis) growth and behavior. *RMBL Student Papers*.

Solomon, N. G. (1994). Effect of the pre-weaning environment on subsequent reproduction in prairie voles, *Microtus ochrogaster*. *Animal Behaviour*, *48*(2), 331–341. https://doi.org/10.1006/anbe.1994.1246

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., … Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611), 241-. Gale Academic OneFile Select.

Visser, M. E., & Phillip, G. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, *3*(6), 879–885. https://doi.org/10.1038/s41559-019-0880-8

Weir, J. C., & Phillimore, A. B. (2024). Buffering and phenological mismatch: A change of perspective. *Global Change Biology*, *30*(5), e17294. https://doi.org/10.1111/gcb.17294

Wells, C. P., Barbier, R., Nelson, S., Kanaziz, R., & Aubry, L. M. (2022). Life history consequences of climate change in hibernating mammals: A review. *Ecography*, *2022*(6), e06056. https://doi.org/10.1111/ecog.06056

Wells, C. P., Tomalty, K. M., Floyd, C. H., McElreath, M. B., May, B. P., & Van Vuren, D. H. (2017). Determinants of multiple paternity in a fluctuating population of ground squirrels. *Behavioral Ecology and Sociobiology*, *71*(2), 42. https://doi.org/10.1007/s00265-017-2270-z

Wells, C. P., & Van Vuren, D. H. (2017). Female kin density affects offspring sex ratio in an asocial mammal, the golden-mantled ground squirrel, *Callospermophilus lateralis*. *Animal Behaviour*, *134*, 71–77. https://doi.org/10.1016/j.anbehav.2017.10.004

Wells, C. P., & Van Vuren, D. H. (2018). Developmental and social constraints on early reproduction in an asocial ground squirrel. *Journal of Zoology*, *306*(1), 28–35. https://doi.org/10.1111/jzo.12569

Wells, C. P., & Vuren, D. H. V. (2025). *No limit yet to phenological plasticity of reproductive timing in a high-elevation hibernator experiencing earlier springs* (p. 2025.11.19.688555). bioRxiv. https://doi.org/10.1101/2025.11.19.688555

Wheeler, H. C., & Hik, D. S. (2014). Influence of shrub canopies on growth rate and pre-hibernation mass of juvenile arctic ground squirrels. *Wildlife Biology*, *20*(4), 253–258. https://doi.org/10.2981/wlb.00038