

Effects of trophic phenological synchrony or dyssynchrony on maternal investment of a small herbivorous mammal (*Callospermophilus lateralis*).

Introduction

The phenology, or timing of life history events, of a species can be based on various environmental cues including temperature, precipitation, and day length (Menzel & Fabian, 1999). Species typically respond to a combination of these cues by varying degrees, resulting in assorted species demonstrating differential responses to the same set of environmental cues (Renner & Zohner, 2018). As climate change elicits intense effects on temperature and precipitation, species often differ in their phenological shifts, creating the potential for phenological dyssynchrony between trophic levels (Renner & Zohner, 2018). For maximum fitness, a species must be capable of matching the annual timing of their greatest energy requirements to that of peak availability of high quality of food sources (Visser et al., 1998). Across trophic levels, terrestrial primary consumers are exhibiting the largest shifts in phenology, risking dyssynchrony with other trophic levels (Thackeray et al., 2016). Dissolution of the evolutionarily beneficial timing between species is of significant concern in conservation biology, as phenological mismatch can potentially decrease species' persistence.

Plant phenology, including growth period, flowering time, and seed set, are affected by globally changing environmental cues (Inouye, 2008). Human disturbances also have effects in modifying historical habitat and spreading invasive plant species (Lembrechts et al., 2016). The Rocky Mountain Biological Laboratory (RMBL), located in Gothic, Colorado, hosts long term studies documenting measurable changes in plant phenology and community composition in relation to climate change (Inouye, 2008). Based on visual observation, the townsite is currently dominated by the common dandelion (*Taraxacum officinale*), an invasive plant that has been documented in the area as early as 1966 (Carleton, 1966). These changes in the phenology and

composition of plants in such ecosystems could have strong effects on herbivorous species that depend on such vegetation for nutrition.

In the subalpine meadows in and around RMBL, hibernating mammals are shifting their spring phenology in response to climatic variables (Prather et al., 2023). Although these shifts are well documented, consequences of such shifts are unknown, and the synchrony or dyssynchrony between vegetative and small herbivore spring phenology is yet to be explored. While seemingly small, shifts in the phenology, quality, and community composition of the vegetation that serve as staples in a species' diet could potentially affect growth rates (and thus total weight gain), and maternal investment in that species. Growth rates and pre-hibernation weight gain have strong effects on individual fitness and are a major determining factor in overwinter survival (Howland et al., 2024). As such, the heavy reliance of these hibernating mammals on a short plant growing season could potentially put these species at increased risk to human disturbance, climate change, and phenological mismatch.

Although phenological mismatches between consumers and their staple food sources have been well documented in many species groups, particularly avian species (Visser et al., 1998), less focus has been dedicated to herbivorous mammals (Plard et al., 2014; Renaud et al., 2022). This is particularly the case for small mammals. Golden-Mantled Ground Squirrels (*Callospermophilus lateralis*) herein referred to as the GMGS, are an example of an herbivorous hibernating small mammal that has demonstrated spring phenology shifts including early emergence from hibernation and earlier reproduction (Wells and van Vuren, 2018). This early emergence and early reproduction allows much of GMGS life history to be shifted earlier in the summer, including pup birth dates and the female lactation period. Maternal lactation, and therefore maternal investment in young, is the most energetically expensive portion of GMGS life history (Kenagy, 1989). GMGS give birth to and nurse their young in an underground

burrow, or the natal burrow, for a 30 day lactation period (Phillips, 1981). This 30 day period is primarily fueled by maternal foraging and therefore may be strongly affected by vegetative phenological shifts (Kanaziz et al., 2020). In a study conducted in 1966, both observation of feeding behavior in GMGS and inspection of stomach contents identified the common dandelion as a key food source making up approximately 80% of the GMGS diet between the months of June and August (Carleton, 1966).

In this study we made use of two long term datasets: one documenting the phenology and plant community composition of RMBL and surrounding sites, and one documenting the long-term demography of the GMGS population in RMBL. We compared the two datasets to determine if there is a statistically significant relationship between dandelion flowering and GMGS maternal investment during female lactation as measured by GMGS litter mass and pup number upon first emergence from the burrow. This study aimed to assess the current and past trends of synchrony or dyssynchrony between GMGS and invasive dandelions over the last three decades. At the scale of individual maternal investment, analysis was also conducted to determine if there is a statistically significant difference in the level of maternal investment in litters born at different times during the summer relative to dandelion flowering as a food source.

Methods

The Golden-Mantled Ground Squirrel population at the Rocky Mountain Research Laboratory site in Gothic, Colorado (38°58'N, 106°59'W) (2900 m elevation) has been the subject of demographic study since 1990. The habitat of the area is largely a mix of subalpine meadow, spruce forest, and aspen forest. Between the months of May and August, the ground squirrels are observed throughout the day for both behavior and location in 7m x 7m grid squares within the 13-ha site (Aliperti et al., 2021). All squirrels are live trapped with Tomahawk model

201 traps baited using a mixture of black oil sunflower seeds and peanut butter (Howland et al., 2024). Once trapped, they receive uniquely numbered metal ear tags and black dye marks on their dorsal pelage for identification. Reproductive females are scored for signs of lactation (visual observation of nipple size and prominence) and their estimated home ranges are mapped to estimate the date and location of pup emergence from the natal burrow (Wells & Van Vuren, 2018). This information is used to aid in quickly capturing pups within two days of their emergence from the natal burrow to be uniquely marked and massed for initial weight at weaning. Date of emergence, litter location, individual pup weight, and litter number are all recorded at this time. Litter mass is calculated for each litter and used as a measure of maternal investment.

Data on the abundance and timing of plant flowering in permanent plots at RMBL has been gathered every summer by Dr. David Inouye and colleagues since 1973 (excluding 1978 and 1990) (RMBL Flowering Phenology Metadata). The project uses the same transect locations each year to monitor the number of flowers of each species in each plot, with flowers being counted approximately every other day. Twenty-three 2m x 2m plots have been monitored since 1974, but others have been added since: two in 1985, three in 1998, two in 2004, and four in 2017 (RMBL Flowering Phenology Metadata). All available *T. officinale* phenology data for each year of our study was used regardless of how long the plot has been included in the project. *T. officinale* data was extracted from this dataset as follows: plots proximal to the study site (both up-valley and down-valley) were selected and their first flowering, median flowering, and last flowering were averaged for comparison against the GMGS lactation period. The plots selected were in the Rocky Meadow (RM), Wet Meadow (WM), and Willow - Meadow Interface (INT) around the Gothic townsite.

GMGS eat the the stems and bases of the flowers and seed heads of the dandelion (Carleton, 1966), and, therefore, dandelion availability as a food source may peak at peak flowering and remain constant as flowers go to seed. The phenology data we used was recently published and includes information on first, median, and last flowering of dandelion plants in the plots, as well as peak abundance data (Prather et al., 2023). We measured synchrony and dyssynchrony between these two trophic levels in two different ways: firstly a simple “distance from a peak” availability measure, and secondly a measure of overlap in lactation period and dandelion flowering period. The distance from peak measure which was calculated using average median dandelion flowering and individual litter emergence dates (end of lactation period) as absolute measures with positive values indicating dandelion availability before the end of lactation period and negative values indicating dandelion availability only after the end of lactation period. This variable was named “synch.” The second type of measure explored overlap in the two periods. Dandelion flowering ranges were bounded by average first flowering and average last flowering, whereas lactation period was bounded by birth day and emergence day. Birth day was estimated by subtracting the 30 day lactation period. It was determined that there are six categories that encompass all ways in which the lactation period and flowering period could be related temporally. These categories include “distance_before”, “overlap_start”, “overlap_end”, “distance_after”, “complete_tarax”, and “complete_lactation” as graphically depicted in Figure 1. The “distance_before” measure quantifies the distance between dandelion availability and lactation period if dandelion availability is before the lactation period. The “overlap_start” measure quantifies the number of days dandelion flowering overlaps with the beginning of the lactation period. The “overlap_end” measure quantifies the number of days dandelion flowering overlaps with the end of the lactation period. The “complete_tarax” measure was calculated when the entire dandelion flowering period was captured by the lactation period

and the “complete_lactation” measure was calculated when the entire lactation period was captured by dandelion flowering. All of these measures were condensed into a single measure named “overlap_distance.” Positive values indicated days overlap of the range regardless of overlap type (overlap_start, overlap_end, complete_tarax, complete_lactation), and negative values indicated the number of days distance between ranges (distance_before, distance_after).

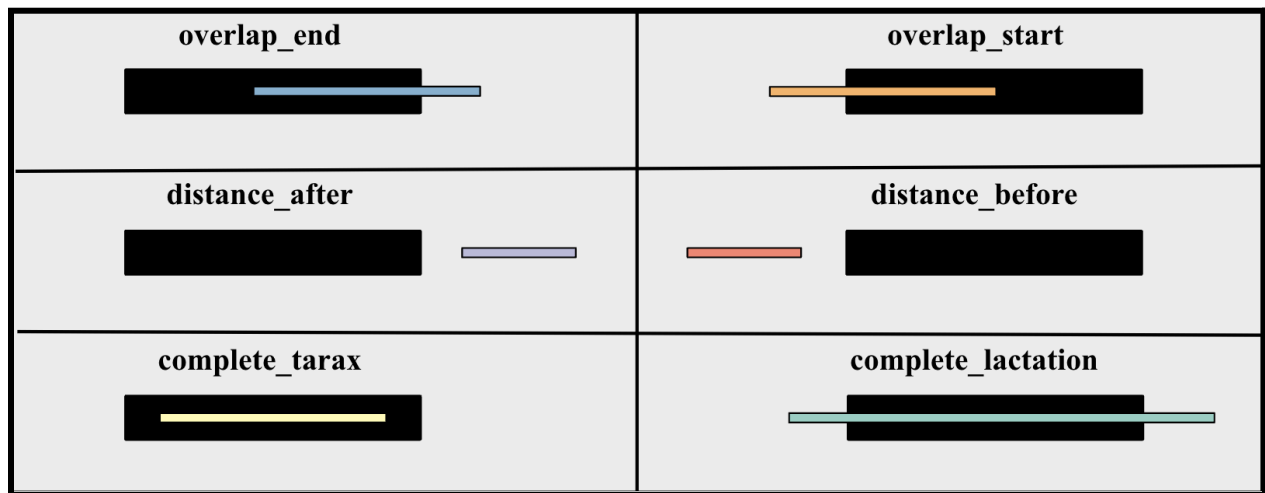


Figure 1: Visual representation of overlap types. Black bars represent the 30 day lactation period, colored bands represent dandelion flowering ranges.

To determine long term phenological match or mismatch, both annual median GMGS emergence date and median dandelion flowering date were graphed across the last three decades (data from 1996 - 2020). At the scale of individual maternal investment, linear mixed models (LMEM) were constructed to detect potential effects of dandelion phenology on GMGS maternal investment (data from 1996 - 2020). We used the R package “*lme4*” to run our models and assign a magnitude and direction of our fixed effects as well standard errors (Bates et al., 2015). The “overlap_distance” measure was determined to be a better measure of synchrony than the “synch” measure using the corrected Akaike Information Criterion for LMEM model selection. We performed a linear mixed effects analysis of the relationship between “litter_mass” and “overlap_distance” as well as “litter_size” and “overlap_distance”. We used “overlap_distance”

and “maternal_age” as fixed effects in both our models. We used “unique_female_ID” and “year” as random effects with no interaction in both our models. P-values were obtained by running the model in conjunction with the lmerTest function.

Results

From 1975 to 2020, *T. officinale* average median flowering dates ranged from ~26 to ~67 days after April 30. Average Median flowering shows a distinct trend towards earlier phenology from 1975 - 2005, and a distinct trend towards later phenology from 2005 - 2020 (Figure 2).

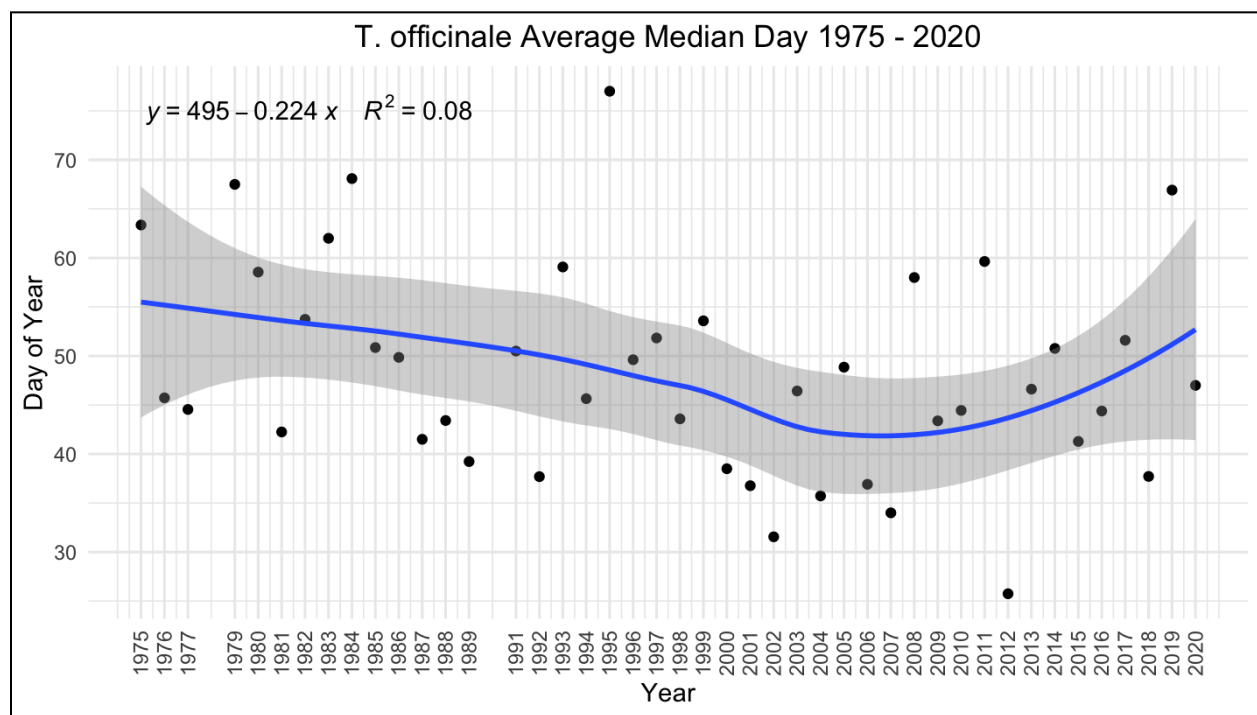


Figure 2: *T. officinale* Average Median flowering shows two distinct trends over the course of available phenology data (1975 - 2020)

From 1996-2020, GMGS first litter births ranged from 10 days to 52 days after April 30. When GMGS Litter First Birth Day is compared to *T. officinale* Average First Flowering Day each year (1996 - 2020), the start of the lactation period occurs before first *T. officinale* availability in 80% of years (Figure 3). The dates of GMGS Litter First Births slightly advanced

over the period ($y = -0.2031x + 439.18$, $R^2 = 0.0236$) while the dates of *T. officinale* Average First Flowering were slightly delayed over the period ($y = 0.089x - 140.01$, $R^2 = 0.0045$); overall, the number of days between First GMGS Birth and First Flowering increased ~ 2.8 days per decade.

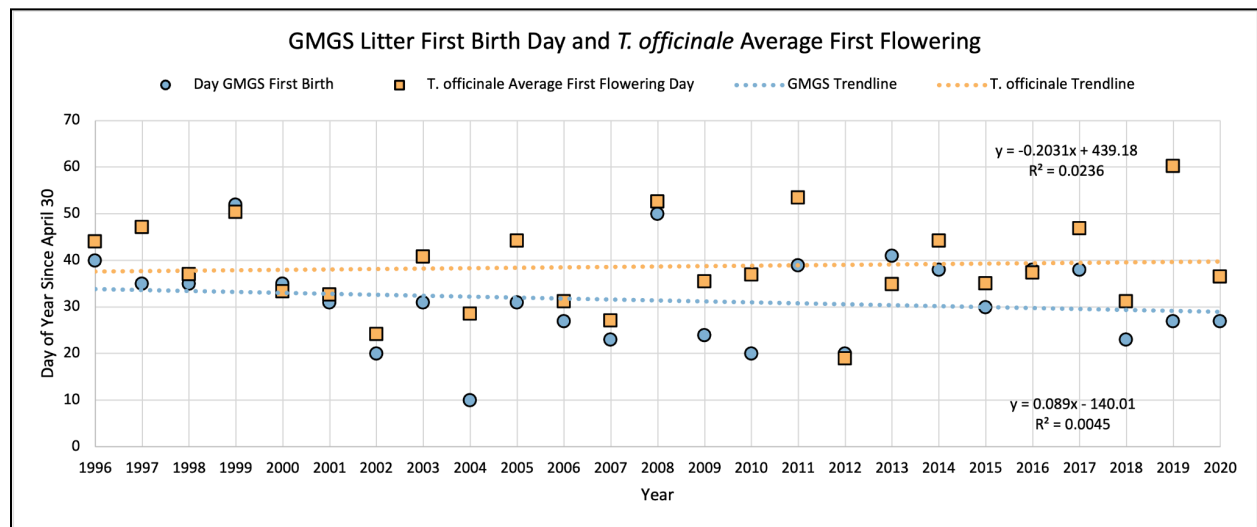


Figure 3: GMGS Litter First Birth Day and *T. officinale* Average First Flowering Day each year (1996 - 2020)

From 1996-2020, GMGS median emergence date ranged from 59 days to 84 days after April 30. When Median GMGS Emergence Day is compared to *T. officinale* Average Median Flowering Day each year (1996 - 2020), Average Median *T. officinale* availability occurs before Median Emergence Day in all years tested (Figure 4). Median GMGS emergence dates slightly advanced over the period ($y = -0.1515x + 375.57$, $R^2 = 0.0278$) while *T. officinale* average median day slightly delayed ($y = 0.2075x - 371.72$, $R^2 = 0.0265$) showing convergence at a rate of ~ 3.4 days per decade.

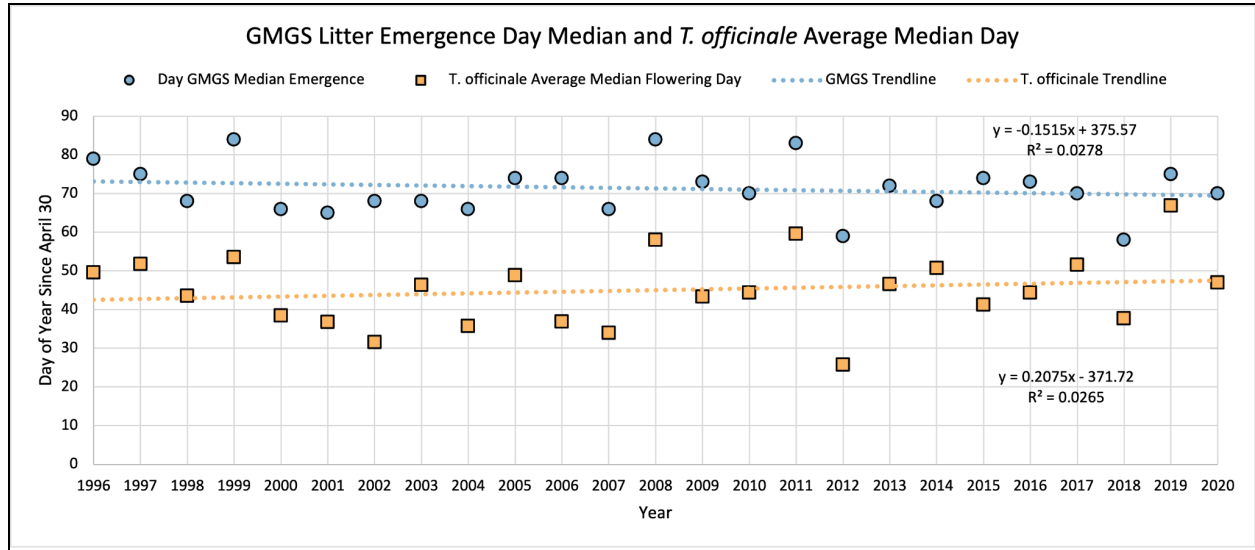


Figure 4: GMGS Emergence Day and *T. officinale* Average Median Flowering Day (1996 - 2020)

From 1996-2020, GMGS last emergence date ranged from 68 days to 110 days after April 30. When GMGS Last Emergence Day is compared to *T. officinale* Average Last Flowering Day each year (1996 - 2020), Average Last Flowering Day occurs before last litter emergence in all years tested (Figure 4). GMGS Last Emergence dates are slightly delayed over the period ($y = 0.2669x - 444.82$, $R^2 = 0.0166$) as are *T. officinale* Average Last Flowering Day ($y = 0.5559x - 1062.3$, $R^2 = 0.137$). *T. officinale* last flowering day and GMGS Last Emergence Day are converging at a rate of ~2.8 days per decade.

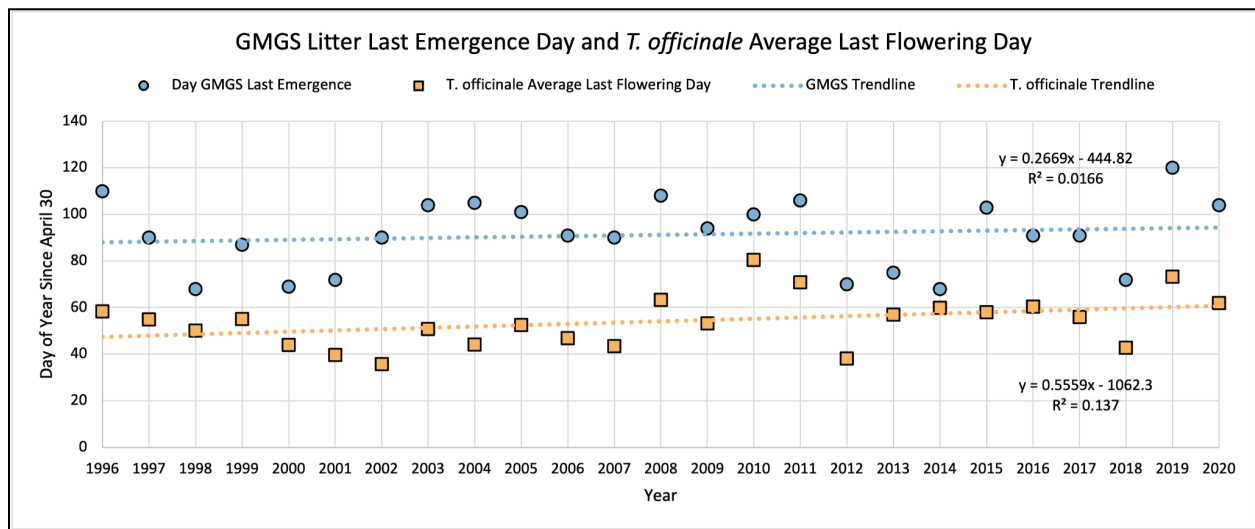


Figure 5: GMGS Last Emergence Day and *T. officinale* Average Last Flowering Day each year (1996 - 2020)

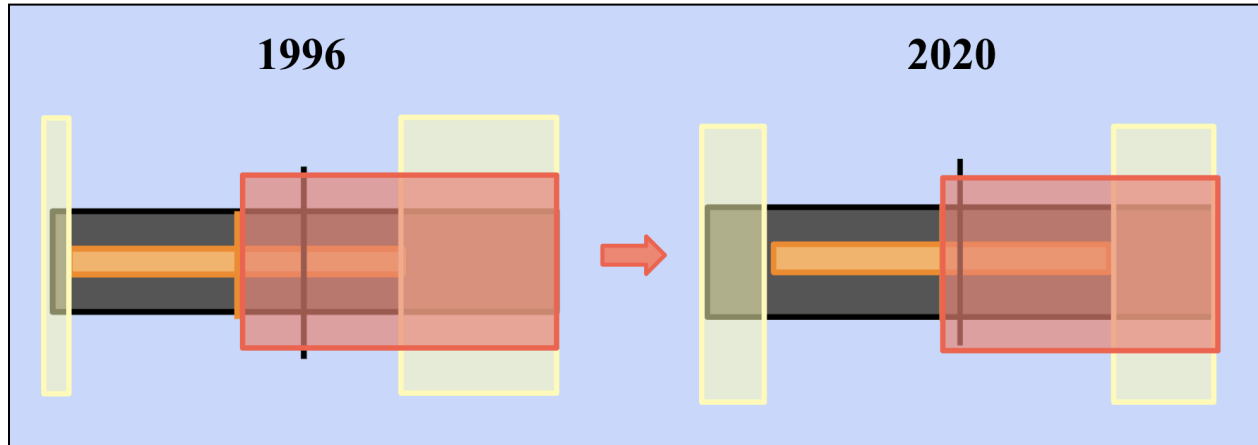
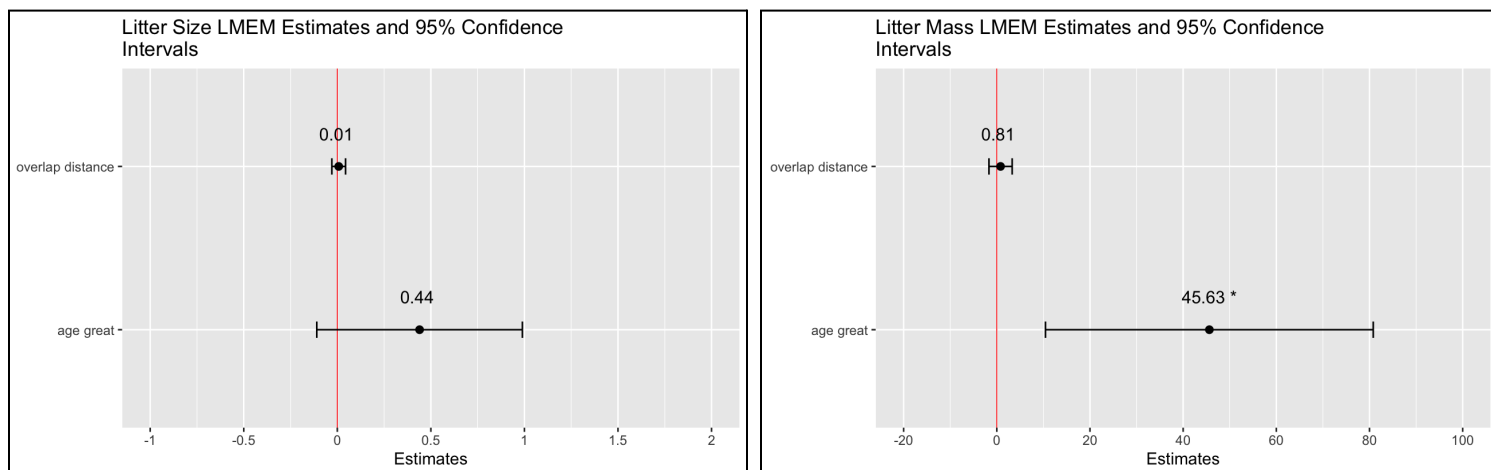


Figure 6: Visual representation of temporal shifts. Black bars represent maternal lactation period, orange bars represent dandelion flowering, transparent yellow represents days between lactation start and dandelion availability as well as lactation end and dandelion availability, transparent red represents day between flowering median and emergence median.

After data cleaning there were 85 complete litters for analysis from 1996 - 2020 (26 years). We found no significant effect of `overlap_distance` measures on litter mass at emergence from the natal burrow ($\beta_{\text{overlap_distance}} = 0.81 \pm 1.25$, $z = 0.65$, $p = 0.521$) (*Figure 5*) or litter size ($\beta_{\text{overlap_distance}} = 0.0075 \pm 0.018$, $z = 0.41$, $p = 0.687$) (*Figure 6*). However, binary measures of maternal age (yearling versus 2+ years) had significant positive effects on litter mass at emergence ($\beta_{2+\text{yrs}} = 45.63 \pm 17.67$, $z = 2.58$, $p = 0.012$). Maternal age (binary) did not have the same significant effect on litter size ($\beta_{2+\text{yrs}} = 0.44 \pm 0.28$, $z = 1.59$, $p = 0.115$). In the litter mass model, random effects accounted for 25.3% of the overall variation in the dataset, with 13.4% attributed to unique female ID and 11.9% attributed to year. In the litter size model, random effects accounted for 5.7% of the overall variation in the dataset, with <1% attributed to Unique Female ID and 5.7% attributed to year.



Figures 7 & 8: Litter Mass and Litter Size LMEM Estimates and 95% Confidence Intervals

Litter mass appeared similar by type of overlap [“distance_before” (N = 1)], [“overlap_start” (N = 9)], [“overlap_end” (N = 37)], [“distance_after” (N = 7)], [“complete_lactation” (N = 4)], [“complete_tarax” (N = 27); Figure 7], although most categories did not contain enough litters for a true statistical test. Similarly, litter size also appeared similar by type of overlap (Figure 8).

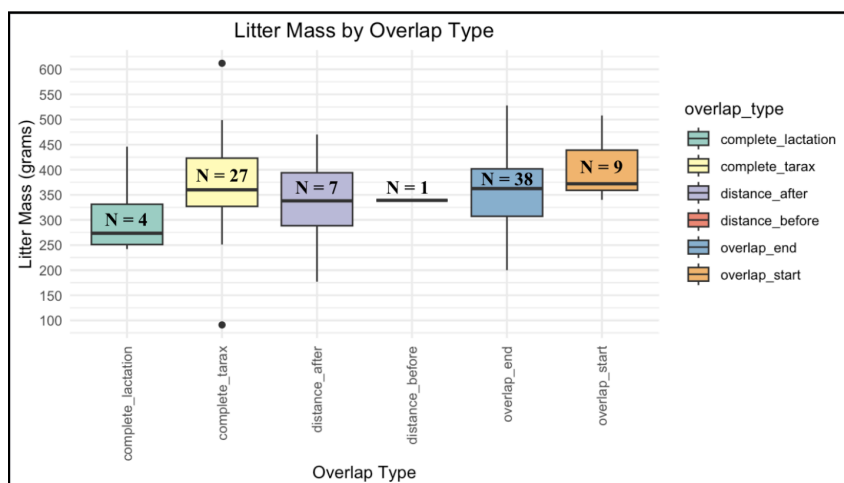


Figure 9: Histogram depicting Litter Mass by Overlap Type

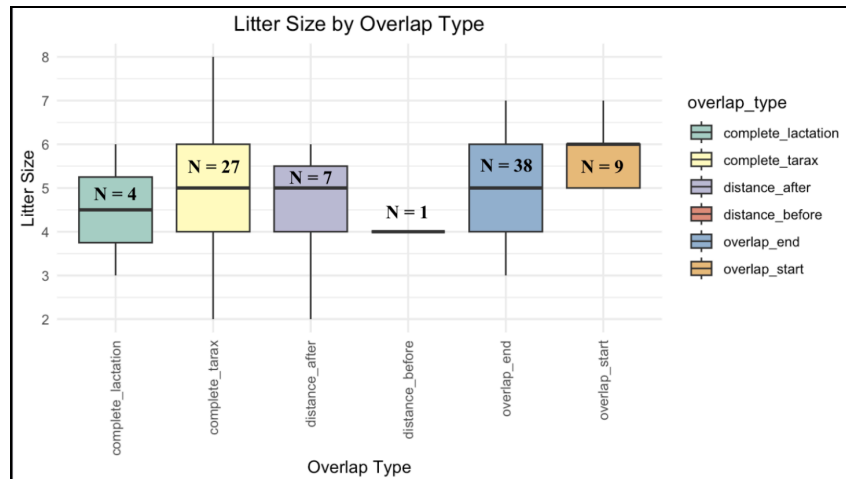


Figure 10: Histogram depicting Litter Size by Overlap Type

Discussion

When looking at the overall temporal shifts of GMGS lactation and their key food resource the common dandelion, GMGS spring phenology is shifting earlier in the season and dandelion is shifting later. Dandelion's shift towards later flowering seems contradictory to widespread trends across species groups to earlier shifts in spring phenology (Prather et al., 2023). Interestingly, over the course of available flowering data (1975 - 2020) we do actually see a general trend towards earlier spring phenology (see also Caradonna et al. 2014). However when constrained to 1996 - 2020 to match available GMGS data, the data shows shifts to later phenology. When making assertions about shifts per decade we assume linear patterns that will continue into the future, however the 1995 - 2020 dandelion data demonstrated that this is not always the case.

The implications of trends seen during the study period on GMGS mean mothers are spending approximately 2.8 more days nursing their young early in the season without dandelion availability as a food source. However, because flowering length remains relatively constant, this also means that there are 2.8 more days of dandelion overlap with lactation later in the season. This might actually be a beneficial outcome given that GMGS experience their highest metabolic

demands towards the end of lactation (Kenagy, 1989). Average median flowering and median litter emergence are also converging, which makes sense as average median flowering occurred before Median Litter emergence in all years studied, and there is an overall shift towards late dandelion flowering. These outcomes could be interpreted as a shift towards more synchrony with the entire lactation period as dandelion availability is shifting to cover the lactation period more evenly.

In match/mismatch papers it is important to determine the study species' peak energy requirement, identify a primary food source, and quantify the timing of that food source (Kharouba & Wolkovich, 2023). Fortunately, this study was able to meet all of those criteria. As far as peak energy requirements, we know when GMGS metabolic requirements peak during the lactation period based on a study using doubly-labeled water (Kenagy, 1989). We also know that approximately 80 percent of the GMGS diet is made of dandelion from a study using observation of feeding behavior and stomach contents analysis of GMGS (Carleton, 1966). We have the privilege of access to long term dandelion flowering data for the entirety of our GMGS data (Prather et al., 2023). Such access to phenology plant information is rare and many studies are required to use proxy data to estimate the timing of food source availability (Plard et al., 2014).

If ground squirrels rely so strongly on a single key food resource (Common dandelion), why did we not detect any changes in investment with changes in that resource availability? One possibility is that flowering may be an incomplete measure of dandelion availability as a food source: though squirrels appear to prefer the flowers, they have also been observed consuming the stems and receptacles of the flowering stalks before, during, and after flowering. Additionally, even though it is preferred by the GMGS it may not be required; dandelion is not a native food source, and though abundant for at least 60 years at this site (Carleton, 1966),

squirrels are known to eat a variety of foods (McKeever et al. 1964). Since the ground squirrels are generalist herbivores, they may be able to easily shift to other sources when needed.

Although this data does not yet exist, a current diet analysis across the season would elucidate when the squirrels are consuming dandelions relative to flowering, as well as, if and when they shift to other food resources.

We considered the possibility that dandelion data used was not representative of what the squirrels are experiencing in their specific home ranges at the spatial level, however a past student project exploring the effects of the spatial distribution of dandelion found no significant effect on mass gain (Spinner, 2022, 2024): reproductive females with more dandelions in their home ranges also did not invest more in their litters or regain more mass before hibernation. According to these two projects in conjunction, it appears that dandelion availability, at both the temporal level as explored by this project, and the spatial level isn't driving key fitness measures in GMGS.

There are many ways to quantify synchrony and dysynchrony between trophic levels (Ramakers 2019). We quantified it in two ways: distance of consumer from a peak of resource availability and overlap in day ranges of consumer and resource, neither of which identified significant effects. Despite being a preferred food resource in the GMGS it does not seem to be driving maternal investment in litters as measured by litter mass or size. Instead, maternal age is a much larger predictor of maternal investment.

Most of our histograms showed too small of sample sizes for true statistical tests of significance between overlap types. The two categories that did have larger numbers of litters were “complete_tarax” (where all of dandelion flowering was captured by GMGS lactation period) and “overlap_end” (where dandelion availability overlapped at the end of the lactation

period). This makes sense as all years except 2010, dandelion had a shorter flowering window than GMGS lactation period, and dandelion is shifting later into the season given relative to GMGS lactation periods. Other categories including `distance_before` and `overlap_start` had very small numbers which makes sense as dandelion flowering seems to be shifting later into the summer. `Complete_lactation` had very few litters as dandelion flowering had smaller ranges than the 30 day lactation period in all years except 2010. I anticipate that we will see a shift of category to more end of season overlap and less early season overlap in the future.

Across Match/Mismatch Hypothesis papers there are quite a few trends for improvement. First there is some question on how well papers address the peak energy requirement, food source, and food source availability as well as how synchrony and dyssynchrony is quantified (Kharouba & Wolkovich 2023). There also is not widespread support of the hypothesis, especially in terrestrial herbivores (Kharouba & Wolkovich 2023). Since so few papers have attempted to quantify the Match/Mismatch hypothesis in terrestrial herbivores, it is important for more studies to evaluate the hypothesis in such systems.

I plan to continue working on this project. I am interested in looking at areas under the curve of dandelion timing and abundance for evaluating synchrony and desynchrony at a finer scale with an abundance component. Although I don't anticipate that evaluating synchrony in this way will show evidence of the Match-Mismatch Hypothesis, I am interested in seeing how different ways of quantifying synchrony or dyssynchrony could affect results. I am also interested in potentially looking at overlap in the last week of lactation as opposed to the entire lactation period as this is the highest energy requirement within the lactation period (Kenagy, 1989) as I see some shortcomings in the way I was able to quantify match or mismatch. To begin with, when I ran my LMER models with the "`overlap_distance`" measure, one day of overlap at

the beginning of the lactation period was treated equally to one day of overlap at the end of the lactation period. Then when I tried to tease types of overlap apart in my histograms, litters with one day of overlap at the end of the lactation period were graphed together with litters that had twenty-two days of overlap at the end of the lactation period. If I were to quantify “overlap_distance” in the last portion of the lactation period, my measures would be subject to the same types of shortcomings, but the effects would be diluted. As one day overlap at the beginning of the shorter period and one day overlap at the end of that shorter period would be fewer days apart and I feel would be similar enough to group together. I am also interested in potentially looking at pre-hibernation weight gain or maternal recovery in weight after the lactation period as a function of dandelion flower availability as a response variable instead of maternal investment in litters. I would also be interested in looking at more independent variables that are affecting maternal investment such as local density. I am also interested in doing some fecal metabarcoding work to reevaluate Carleton 1966 in order to determine what GMGS are eating throughout the season. This would directly determine when the squirrels are eating dandelion relative to flowering, how much dandelion they are eating relative to other food sources, as well as identify sources they may be shifting to when dandelion is not available.

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