

**How do *Bombus appositus* and *Bombus bifarius* worker
tongue lengths vary within a season?**

RMBL Education Program

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ABSTRACT:

Intraspecific trait variation – the variation among individuals within the same species – is seen within all natural populations and strongly affects the dynamics of and interactions between populations, communities, and ecosystems. Individual trait variation fluctuates across space and time, and understanding these patterns can provide a fuller understanding of species ecology and their interactions. Here, we quantified the degree of variation in worker tongue (proboscis) length, across a season within two wild bumble bee species (*Bombus appositus* and *Bombus bifarius*) throughout the Colorado Rocky Mountains. Specifically, we examined how the mean and variation of worker tongue length changes within a season. First, we measured the proboscis length and intertegular distance (ITD) – a strong proxy of body size – of workers. Second, we created an allometric scaling slope between proboscis length and body size to produce a robust estimate of this relationship. Third, we applied this scaling relationship to past *Bombus appositus* and *Bombus bifarius* worker size data from the Rocky Mountain Biological Laboratory to estimate worker tongue length. Fourth, we used the estimated tongue length calculations and measured tongue length values to quantify how *Bombus* worker proboscis length varies across a season. Fifth, we used the estimated tongue length calculations and measured proboscis length values to visualize how *Bombus* worker tongue length varies across season and year. When years were pooled together, we found that *Bombus appositus* worker tongue length increases over a season, but *Bombus bifarius* worker tongue length did not. In addition, we found evidence that supports the hypothesis that *Bombus appositus* worker tongue length inconsistently varies each year across a season, with a similar trend seen for *Bombus bifarius*. Our findings suggest that tongue length may be a consequence of the developmental environment rather than a life history strategy, since no consistent pattern of variation across seasons was observed. These results may have major implications for the future since tongue length mediates the ecological niches species occupy, plant-pollinator interactions, and community dynamics, and if tongue length is changing, these structures and networks may vary as well. Further work is required to confirm the mechanisms that are driving this intraspecific trait variation across a season.

Keywords: intraspecific variation, *Bombus appositus*, *Bombus bifarius*, proboscis length

INTRODUCTION:

Natural populations are composed of phenotypically diverse individuals that interact with their environment in equally diverse ways (Albert, Thuiller et al. 2010, Arroyo-Correa, Jordano et al. 2023). This phenomenon is known as intraspecific trait variation, which may present as variation in morphology or phenology between individuals in the same species. Intraspecific trait variation is advantageous to a species since it can enable individuals to exploit more niches that they would otherwise not be able to exploit if all individuals were morphologically identical (Van Valen 1965). Factors such as the developmental environment, genetic variation, resource availability, climate, or interspecific competition play significant roles in inducing trait variations among individuals within a population (Des Roches, Post et al. 2018, Raffard, Santoul et al. 2019). The distribution of traits within populations is important to consider since it dictates species interactions, population productivity, community and population composition, and long-term coexistence (Bolnick, Amarasekare et al. 2011, Violle, Enquist et al. 2012, Costa-Pereira, Araújo et al. 2019). Therefore, understanding patterns of intraspecific trait variation can advance our mechanistic understanding of processes that drive ecological networks (Jung, Violle et al. 2010, Violle, Enquist et al. 2012, Fajardo and Siefert 2016, Arroyo-Correa, Jordano et al. 2023).

Yet, traits in a population are often considered in aggregate or from single timepoints within a season, assuming that individual variation is constant over space and time (Martin, Rapidel et al. 2017, Souza, Maruyama et al. 2018, Cope, Burkle et al. 2022). However, intraspecific variation is not static in natural populations, particularly for organisms with relatively short lifespans, as the distribution of individual traits within a population may change over time due to ontogeny or phenology (Fajardo and Siefert 2016, Martin, Rapidel et al. 2017). Ontogeny describes an individual's development from egg to adult, while phenology describes the role of timing of an individual's life history events. Temporally variable individuals affect the temporally dynamic ecological communities they are part of by influencing species composition and the niches they occupy, interspecific competition, and network dynamics and links (Junker, Blüthgen et al. 2013, Trøjelsgaard and Olesen 2016, CaraDonna and Waser 2020). Thus, rarely considering temporal variation in ecological studies potentially obscures fundamental

variation that could be utilized for a fuller understanding of the ecological impacts of intraspecies trait variation (Cope, Burkle et al. 2022).

Species with relatively short lifespans may experience more temporal trait variation than species with longer lifespans, as there is greater turnover in the individuals present in a population. For example, in bumble bees (*Bombus* spp.), the colony life cycle is characterized by overlapping generations of workers, such that over the course of the summer months, the population is composed of individuals born at different times (Williams, Thorp et al. 2014). Broods born at different times within the season are subjected to unique larval developmental environments, including climate and diet, which directly influences the morphology of that individual (Sutcliffe and Plowright 1988, Fitzgerald, Ogilvie et al. 2022). These physical traits, such as body size and tongue length, dictate how species interact within their communities and the networks they are part of (Kendall, Rader et al. 2019, Kardum Hjort, Smith et al. 2023).

Since the environment varies across a season, it would be expected that the developmental environment, along with an individual's morphological traits, would also differ across a season. Prior work supports this – with adequate floral resources, worker body size increases within a season, with species differing in body size increase rates (Knee and Medler 1965, Sutcliffe and Plowright 1988, Fitzgerald, Ogilvie et al. 2024). Bumble bee body size is positively correlated to tongue length (Cariveau, Nayak et al. 2016, Melin, Krenn et al. 2019). Therefore, it is likely that bumble bee proboscis length may also vary temporally, consequently shifting the trait distribution within the population across a season. Varying tongue length amongst individuals may have consequences for species foraging as proboscis length is a significant determinant of which floral resources an individual is able to forage for nectar on as individuals can only reach nectar from corollas (petals) as deep as the length of their tongues (Stang, Klinkhamer et al. 2006, Fitzgerald, Ogilvie et al. 2022, Kardum Hjort, Smith et al. 2023). Tongue length alone does not determine which floral resources an individual will or can forage on, as body size and weight (Harder 1983, Harder 1985), proboscis diameter, foraging efficiency (Ranta and Lundberg 1980), flowering phenology (Junker, Blüthgen et al. 2013), and floral morphology (i.e., corolla depth and width) (Harder 1985, Junker, Blüthgen et al. 2013) also significantly determine plant-pollinator interactions.

However, proboscis length imposes strong foraging limitations on individuals and thus heavily influences individual ecological niche-breadths (i.e., an individual's role in their community) (Junker, Blüthgen et al. 2013). Therefore, differences in tongue lengths between individuals within a population are important since tongue length influences floral foraging, pollinator competition, and plant-pollinator networks (Inouye 1980, Klumpers, Stang et al. 2019).

Here, we examined intraspecific trait variation within a season in a population of *Bombus appositus* and *B. bifarius* in the Colorado Rocky Mountains, USA. *Bombus appositus* is a large and long-tongued bumble bee species, while *Bombus bifarius* is a small and short-tongued bumble bee species. We considered worker bumble bee tongue lengths to specifically ask: (1) is there temporal variation in both mean trait values and trait variation? And (2) if so, how does both mean trait values and the degree of variation of tongue length change across time? Using a temporally explicit approach allows us to improve our understanding of how trait-mediated interactions are structured and its consequences for species ecology.

Ontogeny or phenology may independently influence the distribution of tongue lengths within a species. If trait variation is consistent across time, there may be a conserved trait optimum (i.e., an ideal tongue length) or there may be limited developmental flexibility (i.e., constrained proboscis length variability) (H1). However, if temporal trait variation is observed and the pattern of variation is inconsistent across years, it may be a consequence of differences in the developmental environment (ontogeny) each season (H2). This result might indicate that trait variation is a consequence of environmental variation, either within that season or previous seasons (Sutcliffe and Plowright 1988, Guiraud, Cariou et al. 2021). Alternatively, if trait variation is observed and the pattern of variation is consistent across years, this may suggest a life history strategy (phenology) as a response to floral resources changing across time (H3). This result could be due to future variation that is either driven by the resources available at the time of larval development or by an adaptive pressure to respond to future floral resources available to the colony (Prather, Dalton et al. 2023).

METHODS:

Data collection

We non-lethally captured and measured wild *Bombus appositus* and *B. bifarius* workers across seven weeks (from June 26 to August 2) at five established sites near the Rocky Mountain Biological Laboratory in the Gunnison National Forest, Colorado, USA. These sites included Washington Gulch, Rustler's Gulch, Brush Creek, Stupid Falls, and Kebler Pass. *Bombus appositus* forage on many of the common and abundant floral species in the Rocky Mountains such as *Delphinium barbeyi*, *Aconitum columbianum*, and *Vicia americana* (Wright 1988), while *Bombus bifarius* mainly forage on other common floral species in the area, such as *Potentilla fruticosa* and *Erigeron speciosus* (Arrowsmith K. and Stone M., unpublished data). We captured at least ten *Bombus appositus* and *B. bifarius* workers at each site using an insect net. After catching a worker, we placed the individual in a vial labeled with the time of capture and the flower they were caught on. We then placed each vial in a cooler where individuals were kept until they were induced into a chill coma – a reversible physiological state brought on by exposure to cold temperatures (Hazell and Bale 2011). Once in a coma, we removed workers from the vial and measured their tongue length and intertegular distance (ITD, i.e., the distance between the wing bases) – a robust proxy for overall body size (Cane 1987). We measured tongue length by gently extending the individual's proboscis with a tweezer to expose the glossa and proboscis and then measuring the total length of the proboscis with a digital caliper. After completing all measurements, we left the individual in the sun to recover, and they were free to leave once they were ready.

Data analysis

We analyzed *Bombus appositus* and *B. bifarius* separately, and all analyses were conducted in *R* (version 4.4.1). We first calculated separate allometric scaling slopes to predict the tongue length of a *Bombus appositus* and *Bombus bifarius* worker based on its ITD using the data we collected in 2024. Proboscis length and ITD are strongly correlated with each other (Cariveau, Nayak et al. 2016). We created each scaling slope using a standardized major axis (SMA) estimation, which calculates a line of best fit between two interchangeable axes, using the *smart* (version 3.4-8) package. This differs from an

ordinary least squares (OLS) approach using linear regressions, where one variable is predicted from another. This approach generated a scaling slope for each species. If $\alpha = 1$, this indicates that there is an isometric or proportional scaling between two traits. If $\alpha > 1$, this indicates that there is a hyper-allometric scaling slope, where proboscis length increases at a faster rate than body size (i.e. bigger bumble bees have proportionally longer tongues). If $\alpha < 1$, this indicates that there is a hypo-allometric scaling slope, where proboscis length scales at a shallower rate than body size (i.e. bigger bumble bees have shorter tongues). Our analysis produced a scaling slope where $\alpha = 1.93$ for *B. appositus* and a scaling slope where $\alpha = 1.31$ for *B. bifarius*, suggesting that there is a hyper-allometric scaling slope for both species.

These scaling slopes were necessary to create since we applied them to Jackie Fitzgerald's dataset – which is composed of three years' worth of highly resolved data on multiple *Bombus* species' body size measurements collected across multiple study sites near RMBL within a summer season. We then estimated the tongue length of each individual from our allometric scaling estimations. We used both the estimated tongue lengths and measured tongue lengths to create a proboscis length dataset with four years' worth of data.

Tongue length variation

After combining the estimated and measured tongue length datasets for *B. appositus* and *B. bifarius*, we then analyzed tongue length variation across a season in each species separately. Specifically, using R, we calculated both mean and variance of worker tongue lengths for *B. appositus* and *B. bifarius* separately. Proboscis length variance was calculated by using the coefficient of variation, which is *standard deviation/mean*, using the *goeveg* package (version 0.7.5). Then, we used a simple linear model to separately quantify how both mean and variance of worker tongue length varies within a season across weeks. We also used an interactive linear model to quantify how mean worker proboscis length for each species varies across years within a season.

RESULTS:

Allometric scaling model

We measured the proboscis length and ITD of 120 *Bombus appositus* and 144 *B. bifarius* workers. From this dataset we produced an allometric scaling model for both species. *Bombus appositus* worker tongue length increases by 1.93 mm with each mm increase in ITD ($p = 1.98 \times 10^{-5}$), while *B. bifarius* worker tongue length increases by 1.31 mm with each mm increase in ITD ($p = 2.59 \times 10^{-11}$) (Table 1, Figure 1). In other words, larger workers have proportionally longer tongues than smaller bees across species.

Mean tongue length variation across a season

Our final dataset used to analyze temporal proboscis variation consisted of four years and 284 *Bombus appositus* and 494 *B. bifarius* measurements. *Bombus appositus* worker proboscis length increased by 0.21 ± 0.04 mm ($p = 6.66 \times 10^{-7}$, $R^2 = 0.081$) every week when years were pooled (Figure 2, Table 2). *Bombus bifarius* worker tongue length did not vary (0.008 ± 0.014 mm, $p = 0.55$, $R^2 = -0.0013$) across a season when years were pooled (Figure 2, Table 2).

Degree of variation (coefficient of variation) of tongue length across a season

The degree of variation of *Bombus appositus* worker tongue length did not vary (0.01 ± 0.01 mm, $p = 0.65$, $R^2 = -0.179$) over a season when years were pooled (Figure 3, Table 3). Similarly, the degree of variation of *Bombus bifarius* worker tongue length did not vary (0.0020 ± 0.0031 mm, $p = 0.53$, $R^2 = -0.056$) across a season when years were pooled (Figure 3, Table 3).

Yearly mean tongue length variation across a season

Bombus appositus worker proboscis length increased by 0.083 ± 0.028 mm ($p = 0.0034$, $R^2 = 0.13$) over a season when years were considered separately (Figure 4, Table 4). *Bombus bifarius* worker tongue length marginally varied (0.020 ± 0.013 mm) across a season when years were considered

separately ($p = .13$, $R^2 = 0.036$) (Figure 4, Table 4). Both species experienced differing tongue length variation across a season each year, with some years showing a negative sloping relationship between proboscis length and week, while other years showed a positive sloping relationship. In addition, varying years also indicated that year is predictive of the relationship between tongue length and week.

Timeline

I collected data from June 26 through August 2. I visited each site once a week during that period. I analyzed this collected data the following weeks until August 7. During this time, I also produced a presentation and paper explaining my work and results.

DISCUSSION:

Temporal variation of traits within a population has strong ecological consequences, such as impacts on intraspecific and interspecific interactions, community and environmental dynamics, and a species role within a community (Bolnick, Amarasekare et al. 2011, Souza, Maruyama et al. 2018). Understanding how traits within species differ over time allows a greater understanding of more ecological processes. Here, we find species-specific variation in temporal trait variation in a key functional trait in a wild pollinator group.

Our findings showed a strong correlation between body size and proboscis length and strong species-specific patterns of temporal variation for *Bombus* worker tongue length. Specifically, our allometric scaling model showed *B. appositus* and *bifarius* worker tongue length is correlated with ITD, with *B. appositus* worker tongue length increasing faster with each mm increase in ITD than *bifarius* workers. Regarding worker tongue length temporal variation, *Bombus appositus* worker tongue length increases over a season when years were pooled together and when analyzed separately. *Bombus bifarius* worker tongue length did not vary across weeks when years were considered in aggregate but did vary when years were analyzed separately. In addition, both species demonstrated no change in the degree of variation of tongue length (as measured by the coefficient of variation) across a season. Our results

emphasize the importance of considering temporal intraspecific trait variation, as this trait within species can fluctuate over various time scales in different ways.

Several factors would indicate that *B. appositus* worker tongue length variation is a consequence of the developmental environment (ontogeny) (H2), rather than as a result of a life history strategy (phenology) (H3). First, *B. appositus* worker proboscis length increased across a season, suggesting that there is not a conserved trait optimum. Second, *B. appositus* worker proboscis length inconsistently varied across years within a season, with some years indicating an increase in tongue length, while others suggested a decrease in tongue length across a season. If similar yearly seasonal variations in tongue length were observed, it might suggest a life history strategy to produce longer-tongue workers later in the colony life cycle, but instead our results suggest this variation to be a consequence of developmental variation for *Bombus appositus*. These results are also plausible since floral composition and abundance greatly varies across a season; thus pollinators may need to shift which floral resources they are using throughout a season (CaraDonna and Waser 2020).

Our yearly findings may suggest that *bifarius* worker tongue length variation is also a result of the developmental environment (ontogeny) (H2). *Bombus bifarius* worker proboscis length did not consistently vary across a season when years were analyzed separately. Similarly to *Bombus appositus*, our results may suggest that *Bombus bifarius* workers experience tongue length variation across a season due to ontogeny. Across years, *B. bifarius* showed inconsistent patterns of trait variation across weeks. In addition, the observed differences between the *B. appositus* and *B. bifarius* may indicate that they are under different ecological pressures, likely due to their differing morphology.

Implications

Our analysis suggests that the tongue length of *Bombus appositus* and *Bombus bifarius* workers inconsistently varies each year across a season, likely due to ontogeny. These results may have important consequences for *Bombus* species, since proboscis length directly mediates which floral resources a bumble bee can forage on. Specifically, *Bombus* with longer tongues can utilize a wider range of corolla

depths, but their foraging efficiency (i.e., how much energy is required to obtain nectar) is greatest when they forage on flowers with corolla depths similar to their proboscis length (Heinrich 1976, Inouye 1980, Ranta and Lundberg 1980, Arbulo, Santos et al. 2011). Similarly, *Bombus* with shorter tongue lengths have a smaller range of corolla depths they can utilize, but their foraging efficiency is greater when visiting flowers with shorter corolla depths (Inouye 1980, Ranta and Lundberg 1980). Therefore, if intraspecific tongue length is changing across a season from year to year, the ecological niches the species occupies may change across a season as well (Goulson and Darvill 2004). This variation has impacts on pollinator completion, plant-pollinator networks, and ecological community dynamics (Inouye 1980, Fitzgerald, Ogilvie et al. 2022, Kardum Hjort, Smith et al. 2023).

Our findings have important implications for plant-pollinator network studies as well since our results support the notion that plant-pollinator networks and their structures change over the season and vary from year to year. If one node of the network varies or disappears, this will impact the network structure and function. These shifts may also highlight potential forbidden ecological links (Woodard 2017). Therefore, conducting more studies that primarily focus on temporal intraspecific trait variation can help highlight the mechanisms driving network structure and how they change over time. In addition, gaining a greater understanding of how individuals within a species temporally vary can help us better understand how the ecological niches species occupy change over time.

The findings from this work will likely have implications under climate change. Specifically, higher altitude environments are expected to be more heavily impacted by climate change (Engler, Randin et al. 2011). Climate change will impact the natural environment, such as through flowering phenology, floral biodiversity, snowmelt time, weather variability, and warmer temperatures, so it is likely that these environmental changes will also impact bumble bees in species-specific ways (Bakkenes, Alkemade et al. 2002, Pradervand, Pellissier et al. 2014). If ontogeny is the main driver of tongue length variation, then we would expect environments impacted by climate change to impact proboscis length, potentially seeing more extreme temporal variation in tongue length. Prior work has shown that colonies exposed to high temperatures (about 33 °C) produce smaller workers, thus it is likely that higher temperatures will also produce workers with shorter tongues (Guiraud, Cariou et al. 2021). These

morphological changes may disrupt plant-pollinator networks, their structures, and ecological dynamics, having major implications for the structure of these communities (Pradervand, Pellissier et al. 2014). In addition, *Bombus* species are relatively morphologically similar, only with major differences in color, body size, and tongue length (Goulson and Darvill 2004). Therefore, changes in proboscis length will likely have significant species-level and community-level consequences.

To better understand the results of our study, further work should be conducted to better understand the mechanisms driving intraspecific tongue length variation. In addition, studies that consider colony-level variation may be helpful in determining exactly which factors influence tongue length. Both would help expand our knowledge on temporal intraspecific trait variation and therefore further our understanding of ecological networks and their implications. Similar work should be conducted on more *Bombus* species and other pollinators, who also use their proboscis in foraging, since pollination is at the heart of our food systems and overall ecological function.

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TABLES AND FIGURES:

Figure 1. Tongue length and ITD allometric scaling model for *Bombus appositus* and *Bombus bifarius*.

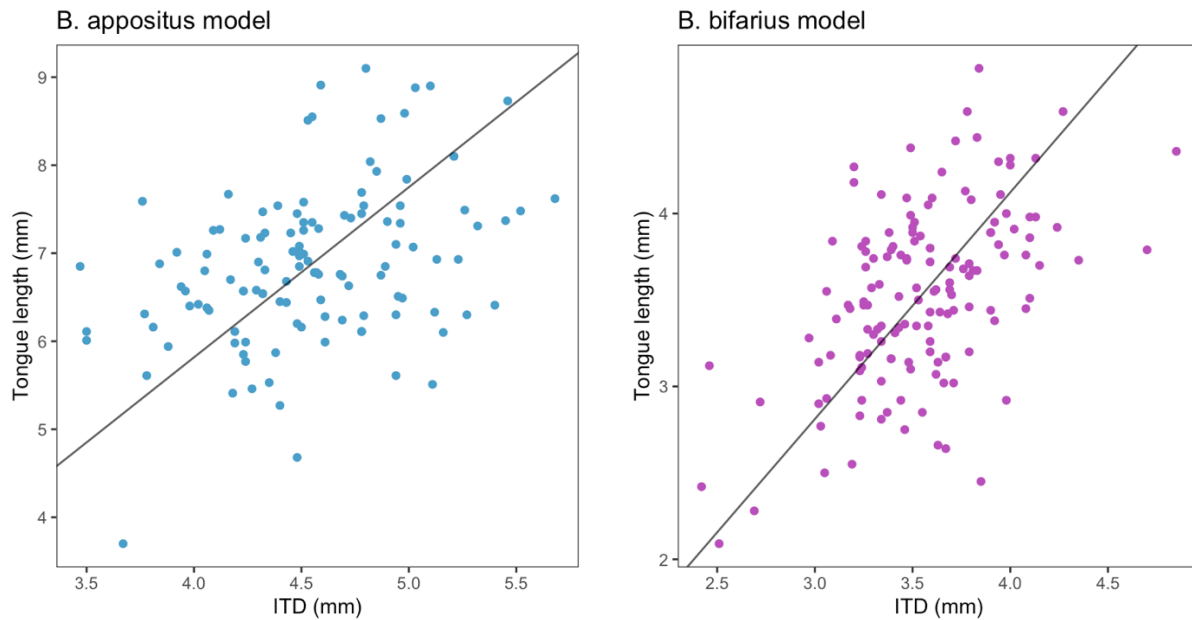


Figure 2. *Bombus appositus* and *Bombus bifarius* tongue length variation by week across a season.

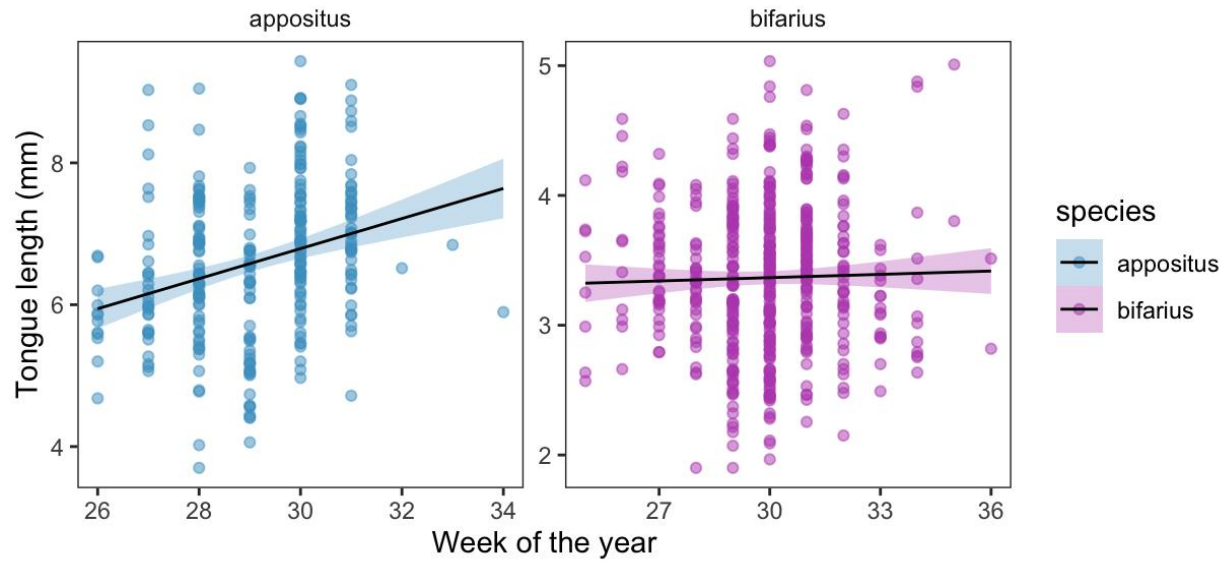


Figure 3. *Bombus appositus* and *Bombus bifarius* proboscis length coefficient of variation by week across a season.

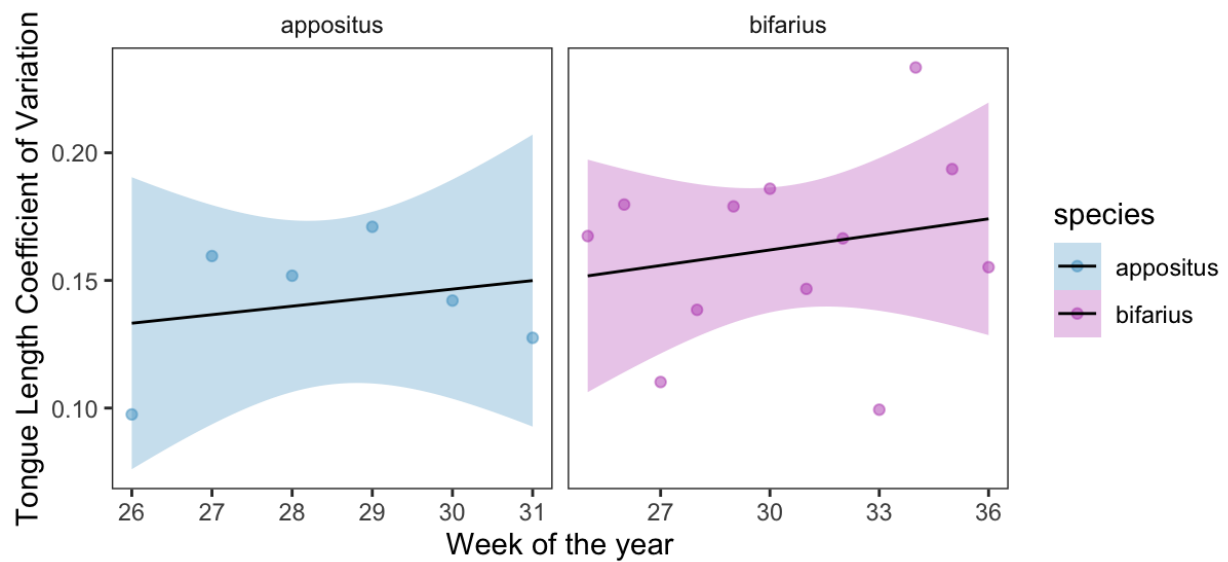


Figure 4. *Bombus appositus* and *Bombus bifarius* tongue length variation across years (2020-2024) and weeks in a season.

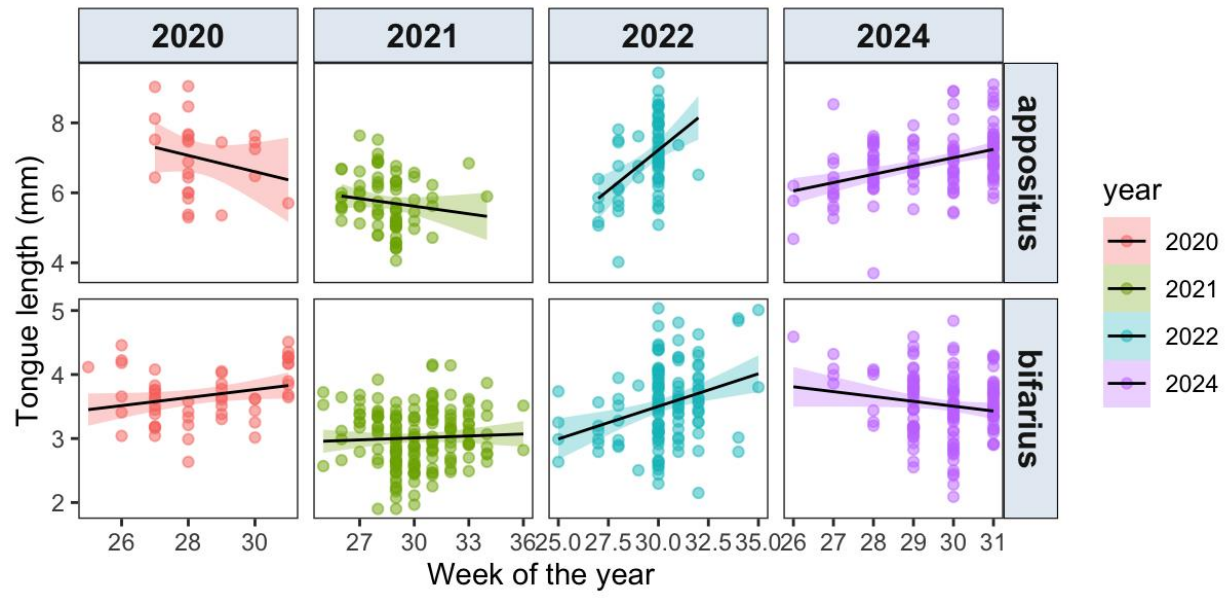


Figure 5. Brush Creek field site.

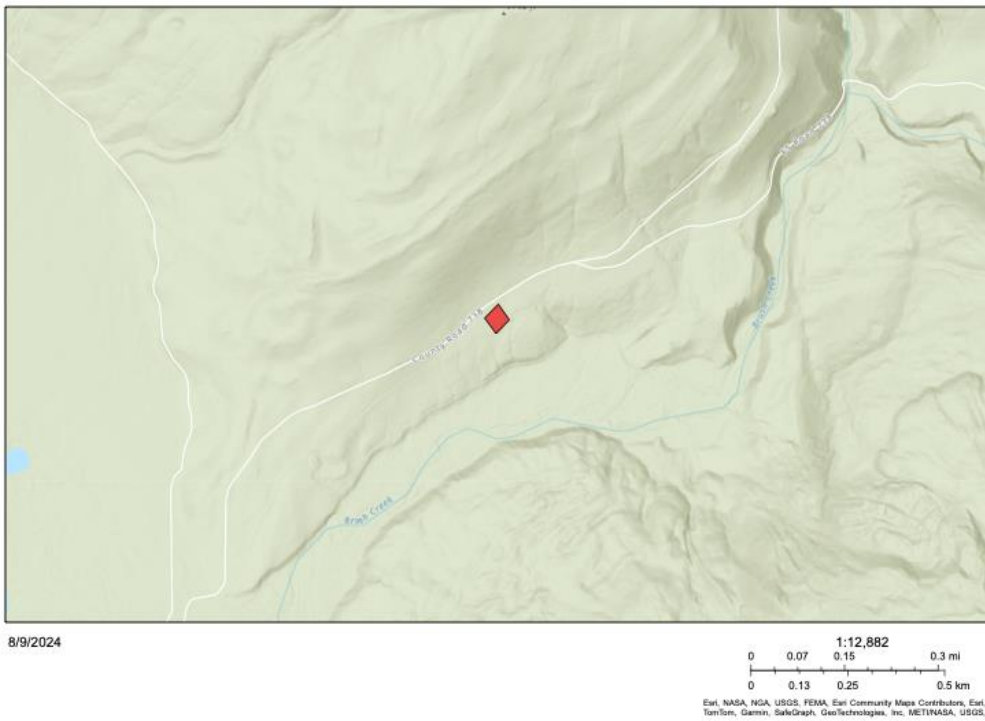


Figure 6. Kebler Pass field site.

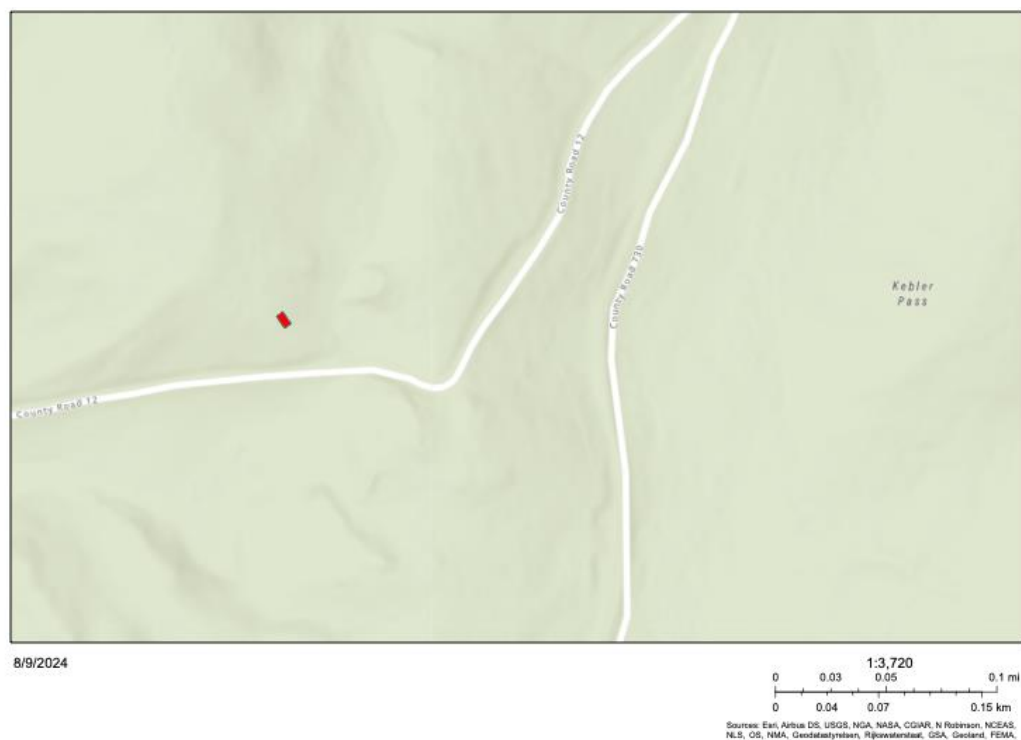


Figure 7. Washington Gulch field site.

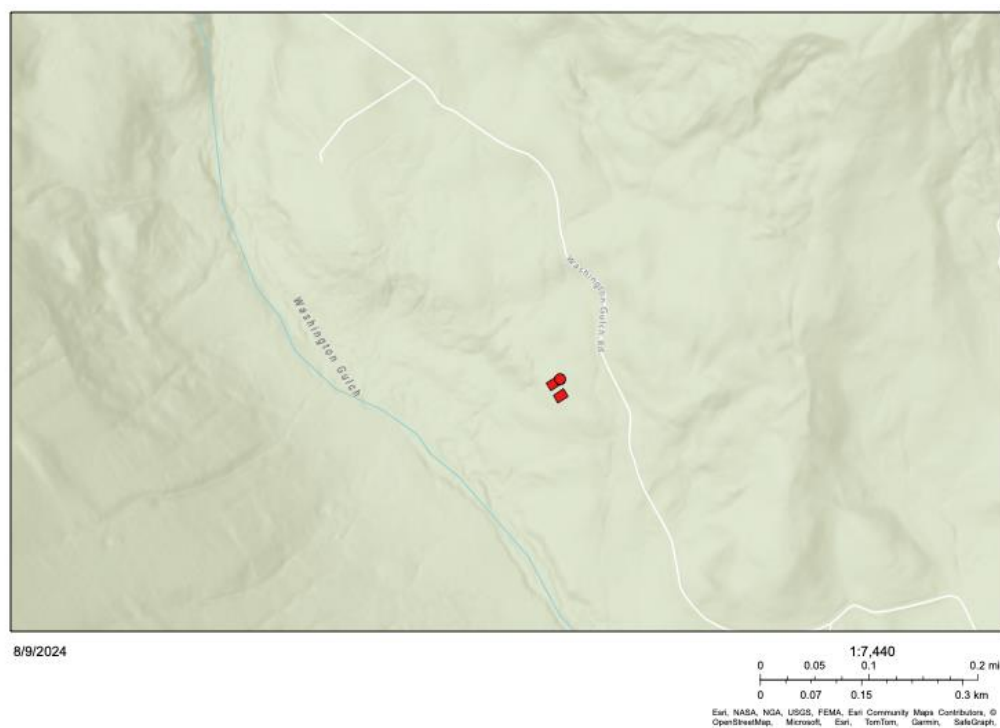


Figure 8. Rustler's Gulch field site.

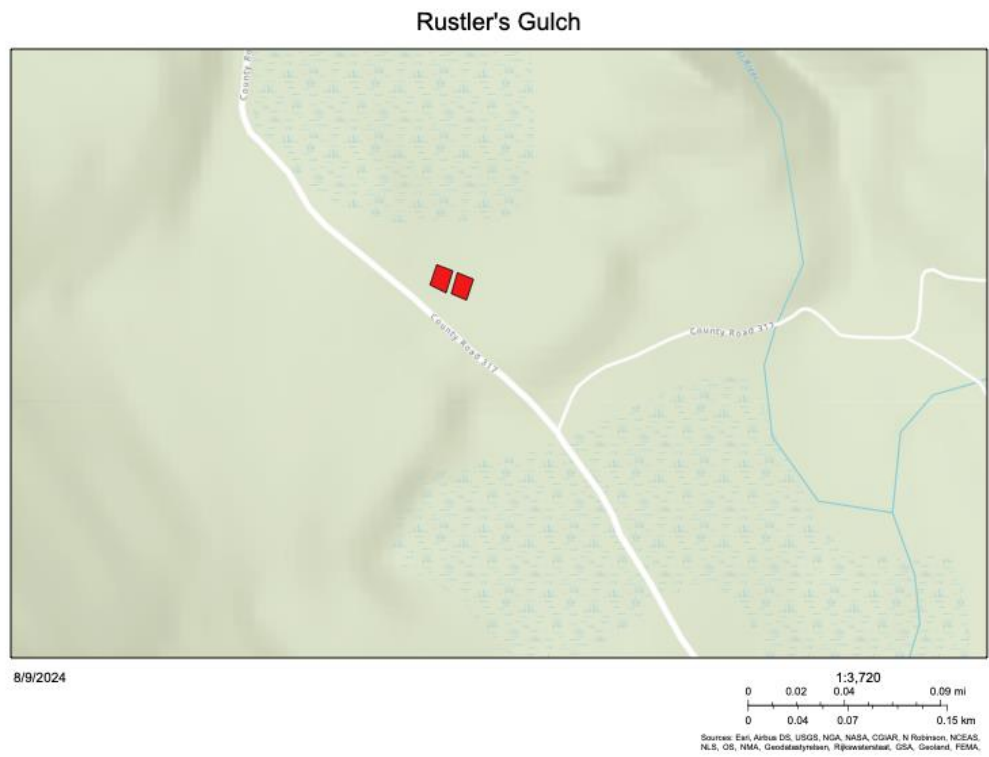


Figure 9. Stupid Falls field site.

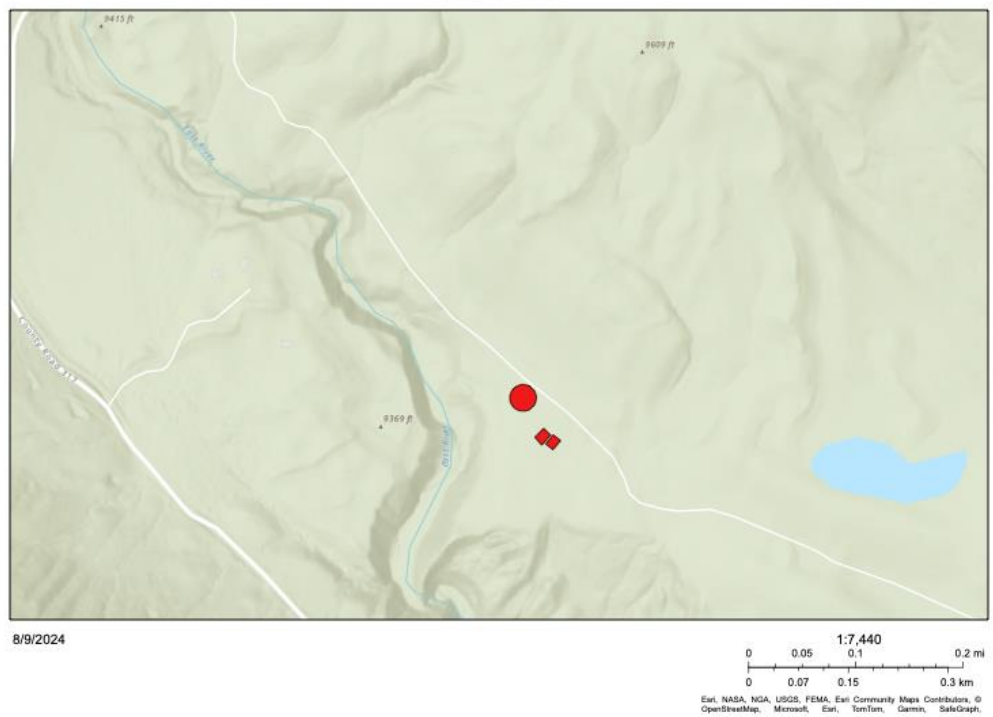


Table 1. Intercept, slope, and p-value, and R^2 for the allometric scaling model for proboscis length and ITD for *Bombus appositus* and *Bombus bifarius*.

Species	Slope	Intercept	P-value	R^2
<i>Appositus</i>	1.93	- 1.92	1.98×10^{-5}	0.14
<i>Bifarius</i>	1.31	- 1.12	2.59×10^{-11}	0.27

Table 2. Intercept, slope, p-value, and R^2 for the linear model between proboscis length and week for *Bombus appositus* and *Bombus bifarius*.

Species	Slope	Intercept	P-value	R^2
<i>Appositus</i>	0.21	0.042	6.66×10^{-7}	0.081
<i>Bifarius</i>	0.0085	0.014	0.55	- 0.0013

Table 3. Intercept, slope, p-value, and R^2 for the linear model between the coefficient of variation for proboscis length and week for *Bombus appositus* and *Bombus bifarius*.

Species	Slope	Intercept	P-value	R^2
<i>Appositus</i>	0.0033	0.0068	0.65	- 0.18
<i>Bifarius</i>	0.0020	0.0031	0.53	- 0.056

Table 4. Term, estimate, standard error, t-value, p-value, and R^2 for the linear model between proboscis length, week, and year for *Bombus appositus* and *Bombus bifarius*.

Species	Term	Estimate	Standard Error	T-value	P-value
<i>Appositus</i>	Week	- 167.72	56.76	- 2.96	0.0034
	Year	- 2.27	0.81	- 2.79	0.0057
	Week*Year	0.083	0.028	2.96	0.0034
	R^2	0.13			
	$F_{3, 280}$	15.59	P-value	2.096×10^{-9}	

<i>Bifarius</i>	<i>Week</i>	- 41.22	27.01	- 1.53	0.13
	<i>Year</i>	- 0.52	0.40	- 1.33	0.19
	<i>Week*Year</i>	0.020	0.013	1.53	0.13
R^2		0.036			
$F_{3, 490}$		7.08	<i>P-value</i>	0.00011	