Responses to Global Change: A Study of Bee Body Size Across a Century of Environmental Variation

Honors Thesis

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Abstract

Bees are vital pollinators, they provide invaluable ecosystem services to humans and play a crucial role in the success of agricultural production and overall ecosystem function. There are over 1,000 species of native bees present within Colorado, many of which are experiencing population declines and morphological changes due to unpredictable climate and ecosystem conditions associated with climate change. This threat to native bees has sparked an increase in research that aims to provide information about species trends over time to better inform conservation efforts. In this study, an intraspecific analysis of three bee species (*Agapostemon texanus, Bombus pensylvanicus, Anthophora montana)* was completed with museum specimens to explore the changes in bee body size over time and how varying climate conditions impact their development. Museum specimens were used to measure intertegular distance (ITD), the distance between tegulae across the thorax as a proxy of bee body size (Cane 1987). Over 180 individuals were measured for each species, all from various dates and locations throughout Colorado and Southern Wyoming, spanning 124 years. After all specimens were measured, a comprehensive analysis was completed to examine bee body size shifts over the course of the collected specimens and correlations with climate. The results indicate a significant decline in body size for *B. pensylvanicus* and *A. texanus*, and a significant increase in body size for *A. montana* over time. *B. pensylvanicus* also showed a significant decrease in size when elevation increases. Further analysis revealed a significant relationship between female *A. texanus* and growing season precipitation. No significant correlation was found between temperature and body size for any species. The results from this study represent a combination of factors resulting in physical adaptations. Ultimately, this study highlights how environmental changes may be

subtly shifting bee morphological characteristics causing adaptations within and across species, which could lead to cascading effects within ecosystems.

Introduction

Attempting to predict how climate change will affect the global biotic environment has been the primary focus of conservation efforts in recent decades. Bee populations are threatened by a variety of factors including human induced habitat loss, increased application of pesticides, and climate change (Brown et al. 2016). Therefore, more regional assessments are needed to provide localized information on species trends and predict future population changes (Nooten and Rehan 2019). Declines in native bee populations are not uniform, and vary depending on species. These declines consequently result in parallel declines in the plants that rely on these pollinators to reproduce (Potts et al. 2010).

In addition to population declines, morphological changes such as size, overall physical condition, and sex ratios have been documented in animals as a response to changing patterns in climate (Verberk et al. 2021, Spinks et al. 2022). In pollinators, bee body size is shifting with changing climate and resource conditions. Factors such as increasing temperatures during development can reduce body size in adult bees (Gerard et al. 2023). Specifically, larger bee species such as *Bombus* have been found to decline in size faster than smaller-bodied species as they adapt to unfavorable conditions (Nooten & Rehan 2019, Oliveira et al. 2016). Bee body size is a key functional trait that reacts to changing resource availability and climate conditions and impacts plant-pollinator interactions (Fitzgerald et al. 2022). The body size of bees is plastic, and is impacted by a variety of factors. For instance, bees with larger body sizes allow for higher pollen loading capacity and more extensive foraging ranges (Greenleaf et al. 2007). *Bombus* specifically have shown significant size variation at the species level and between species (Peat et al. 2005).

Historical data from museum collections suggest a shifting baseline in bee morphology, often following Bergmann's Rule, which assumes that individuals within a species tend to be smaller in warmer environments and lower elevations and larger in colder, higher elevation environments (Kingsolver and Huey 2008). This trend is frequently driven by the metabolic cost of development, warmer temperatures during the larval stage can accelerate metabolism, leading to faster development but smaller adult sizes (Kingsolver and Huey 2008). In North America, studies have already documented significant declines in the average body size of several wild bee species over the last century, correlating strongly with rising mean temperatures and increased frequency of extreme weather events (Gerard et al. 2023).

The ecological consequences of shrinking bee body size extends beyond the individual's success, potentially disrupting the stability of ecosystem health, plant-pollinator interactions, and more. Body size is intrinsically linked to foraging distance, a reduction in size limits the area over which a bee can collect resources (Greenleaf et al. 2007), effectively isolating plant populations that were once connected by larger-bodied pollinators. Additionally, the size relationship between bees and flowers is critical for effective pollen transfer; if bees become smaller while the floral morphology of their hosts remains the same, the efficiency of pollination actions may decline, leading to reproductive consequences for the plants (Kuriya et al 2015).

Methods

Species Selection and Measurement

To assess factors driving morphological shifts, we examined historical specimens of three bee species with varying social structures: *Bombus pensylvanicus* (American bumble bee; n = 183), *Agapostemon texanus* (metallic green sweat bee; n = 239) and *Anthophora montana* (Rocky Mountain digger bee; n = 188). Specimens were sourced from the C.P. Gillette Museum of Arthropod Diversity at Colorado State University, with data managed via the Ecdysis Portal (Ecdysis 2026). All specimens were collected within Colorado and Southern Wyoming between 1898 and 2022. Intertegular distance (ITD), defined as the distance between the wing-attachment points across the thorax, was measured for all bees as a standardized proxy for overall body size. Measurements were completed using digital calipers mounted on a stereomicroscope, recorded to a resolution of ~0.01 mm.

Climate Data Acquisition

Historical climate and elevation data were matched to each specimen based on collection year and coordinates. For specimens lacking exact coordinates (n = 76), county central coordinates were used. Specimens missing both specific and county level location data (n = 8) were excluded from data analysis. Environmental variables were extracted from the PRISM Climate Group (Oregon State University) at a 4 km spatial resolution using the prism package (version 0.3.0) in R. For each unique collection location, monthly values for total precipitation (mm) and maximum temperature (°C) were extracted using the prism package (version 0.3.0) in R.

Statistical Analysis and Visualization

To align climate data with the season of bee development, three monthly values (May, June, and July) were selected for growing season metrics. For precipitation, a growing season total was calculated (mm). For temperature, an average growing season maximum temperature value was calculated (°C). These climate values were matched with the appropriate year (collection year or t-1) for every individual bee. For *B. pensylvanicus* and *A. texanus*, body size was modeled against climate conditions from the same year as collection, as their larval development occurs within weeks of adult emergence. For *A. montana*, body size was modeled against climate conditions from the previous growing season. This accounts for the maternal provisioning hypothesis; the body size of the current year's adults is determined by the resources collected by the mother during the prior year's provisioning phase. This species produces one generation per year, and that generation's success is dependent on the mother's success during the provisioning year (t - 1). A series of linear regression models were used to evaluate the influence of year, elevation, temperature, and precipitation on body size (ITD). Data were visualized using the *ggplot2* and *tidyverse* packages. To account for sexual dimorphism, models were separated for each species and sex. Figures were faceted by species and sex using *facet_wrap* or *facet_grid*. Statistical significance for all models was determined at $p = 0.05$.

Results

A total of 610 bees were measured, and after data cleaning, 479 were used for analysis over a 124 year period. A primary temporal model identified a significant decline in the body size of female *Bombus pensylvanicus* (ß = - 0.00214, p = <0.001; Figure 1) and female *Agapostemon texanus* (ß = - 0.00092, $p < 0.0018$; Figure 1), while *Anthophora montana* exhibited a significant increase in size over the same period (ß = 0.00125, $p < 0.02$; Figure 1). None of the males exhibited statistically significant decreases or increases in body size.

Multiple regression analysis indicated that the drivers of these changes are genus-specific. For *B. pensylvanicus*, elevation emerged as a dominant predictor (ß = - 0.001477,

$p < 0.001$; Figure 2). For climate variables, several analyses revealed that while precipitation showed a slight positive correlation with body size across all species, it was not the sole determinant of size (Figure 3). Female *A. texanus* was the only group that showed a significant relationship between precipitation and body size (ß = 0.00042, p = 0.048; Figure 3). Temperature did not reveal a significant difference in body size across species and sex. Previous year climate data analyzed with *A. montana* revealed a weak positive correlation between body size and previous year precipitation levels, but no correlation was found between body size and previous year temperatures (Figure 5). Neither precipitation or temperature revealed significant relationships with male or female *A. montana* (Figure 5).

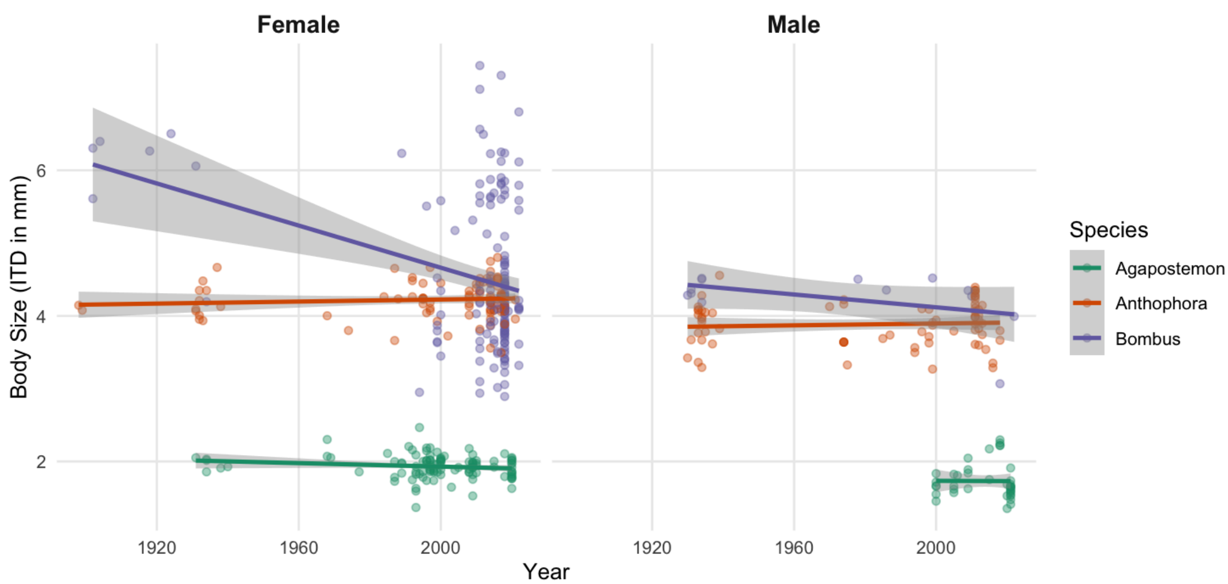

Figure 1. Shifts in bee body size across three species in Colorado and Wyoming (1898–2022). Scatter plots represent individual specimens with linear regression lines indicating temporal trends divided by sex. Significant declines in ITD were observed for female *B. pensylvanicus* (ß = - 0.00214, p = <0.001) and female *A. texanus* (ß = - 0.00092, p < 0.0018), while female *A. montana* exhibited a significant increase in body size over the same period (ß = 0.00125, $p < 0.02$).

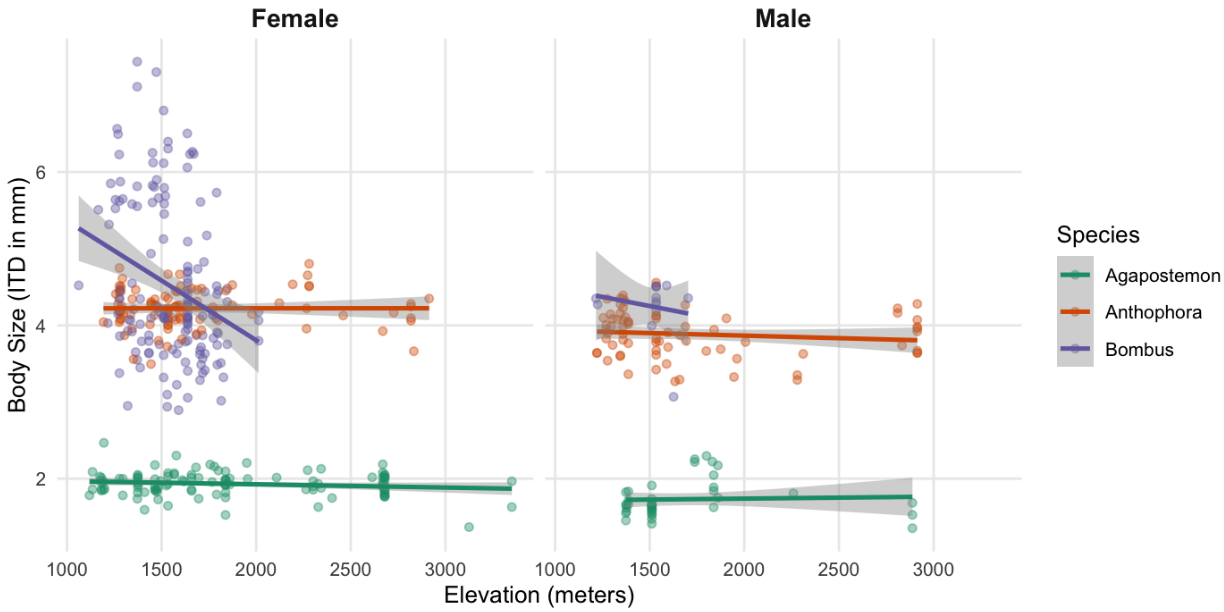

Figure 2. Relationship between elevation and body size in *A. texanus, A. montana,* and *B. pensylvanicus*. Scatter plot illustrates a highly significant negative correlation between intertegular distance (ITD) and elevation ($p < 0.001$) for *B. pensylvanicus.* Correlations between *A. texanus* (p = 0.895) and *A. montana* ($p = 0.381$) with elevation are not significant.

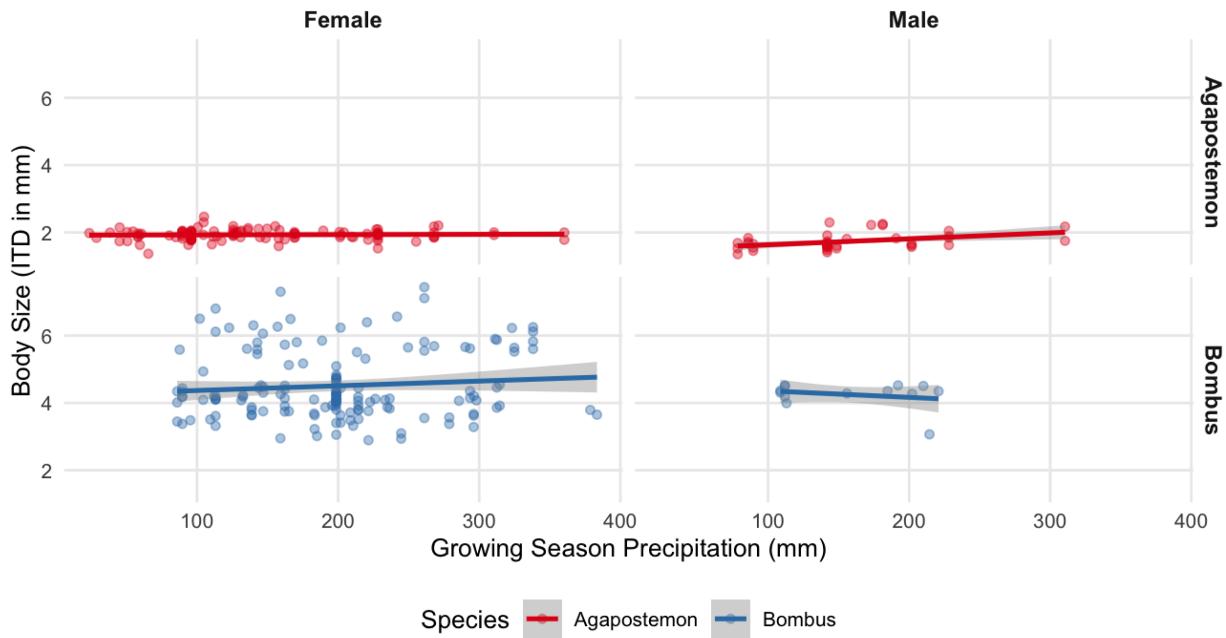

Figure 3. Scatter plot displaying relationship between *A. texanus* and *B. Pensylvanicus* body size and growing season precipitation totals for the year each specimen was collected, in mm. Female *A. texanus* analysis revealed a significant (ß = 0.00042, $p = 0.048$) relationship between precipitation and body size. Specific linear regressions for male *A. texanus* and male and female *B. pensylvanicus* did not reach statistical significance.

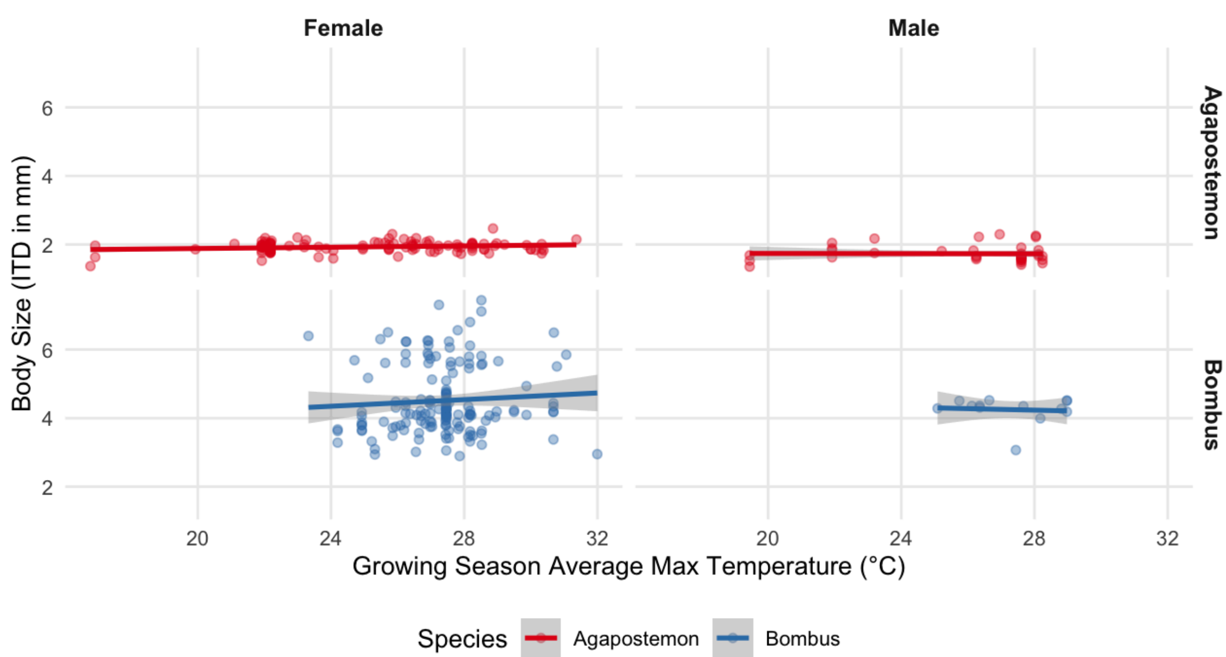

Figure 4. Scatter plot displaying relationship between *A. texanus* and *B. Pensylvanicus* body size and growing season average maximum temperature (°C) for the year each specimen was collected. Neither species nor sex reached statistical significance.

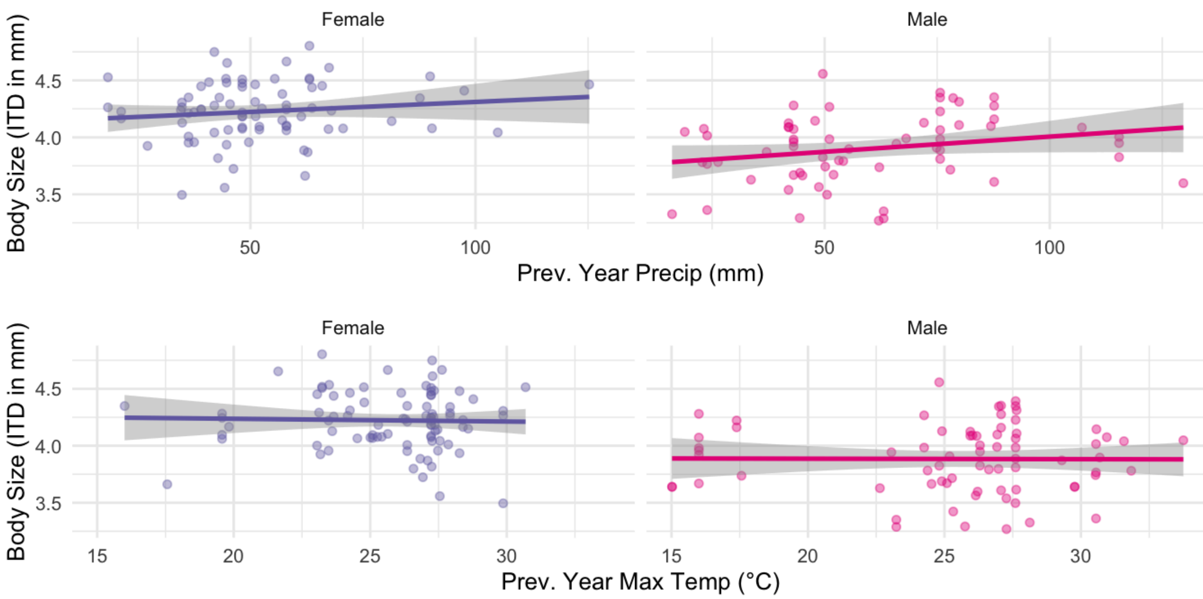

Figure 5. Plot displaying climate effects on body size for *A. montana* separated by sex. Previous year climate conditions were used to account for the overwintering period, as maternal provisioning occurs in the previous year. Temperature (p = 0.804) and precipitation (p = 0.402) showed no significant change in body size.

Discussion

The observed decline in body size for *Bombus pensylvanicus* and *Agapostemon texanus* over the last century suggests that these species are responding to complex environmental pressures. Although the Temperature-Size Rule is often cited as the primary driver of insect shrinkage, the lack of a strong direct correlation with growing season temperatures in this study suggests that pollen limitation and resource availability are more likely the dominant factors (Ogilvie et al. 2017). In the Rocky Mountain region, climate change has significantly altered floral phenology, creating a size relationship shift between bee emergence and the peak bloom of their preferred forage (Rafferty 2017). Because bee body size is largely determined by the amount of resources provided during the larval stage (Cane 1987), a shorter foraging season limits the total energy a bee can invest in its offspring. This can result in smaller body sizes (Nooten and Rehan 2020).

Additionally, the significant decline in size at higher altitudes observed in *B. pensylvanicus* presents a direct challenge to Bergmann's Rule. While Bergmann's Rule traditionally predicts that organisms should be larger in colder, high-elevation environments to conserve heat, some insects exhibit an inverse relationship to Bergmann's Rule (Kingsolver & Huey 2008). High-elevation bees face an extremely narrow developmental window, therefore individuals that reach maturity quickly at a smaller size are more likely to survive than those attempting to reach a larger mass before the first frost. This selection for smaller, faster-maturing bees may be intensifying as mountain climates become more unpredictable (Scaven & Rafferty 2013). Ultimately, the size decline of these pollinators likely reflects a response to many factors. The morphological trends observed in this study suggest that climate change does not produce uniform changes on Colorado's native bee populations. The significant body size declines of *B. pensylvanicus* and *A. texanus* over time supports the Temperature-Size Rule, which posits that warmer developmental environments result in smaller adult body sizes due to accelerated metabolic rates (Kingsolver and Huey 2008). This is particularly concerning for social species like *Bombus*, as smaller body sizes are linked to reduced foraging ranges and lower pollen-loading capacities (Greenleaf et al. 2007). As the climate warms, the flowering season in subalpine environments is shifting and, in many cases, shortening. This contraction of floral resources creates a state of limited pollen resources. This is relevant for a social species like *B.*

pensylvanicus, because a shorter foraging season likely restricts the total energy available, resulting in the production of smaller bees as a survival strategy (Ogilvie et al. 2017).

The significant increase in the body size of *Anthophora montana* represents a notable difference from the general trend of insect size decline under global warming. As a solitary, ground-nesting species, *A. montana* could be buffered from surface temperature extremes, or its specific early-season phenology may allow it to better exploit the increased precipitation and subsequent floral abundance observed in this study. The nonsignificant relationship between precipitation and body size among *B. pensylvanicus* and *A. texanus* suggests that for these species, body size may be more strongly related to other factors like elevation rather than fluctuations in rainfall.

Together, these findings mean that the stability of Colorado's pollinators is being subtly shifted with a changing landscape. If keystone pollinators like *Bombus* continue to shrink, the size relationship between bees and native flora may be disrupted, leading to a decline in pollination efficiency (Kuriya et al. 2015). The varying responses of these three species underscore the importance of moving beyond broad generalizations about bee declines and instead focusing on how specific traits such as sociality, nesting behavior, and sex determine a species vulnerability to a changing climate (Nooten and Rehan 2019).

Limitations

While this study provides a unique perspective on bee morphology, several limitations should be acknowledged. First, the use of museum specimens introduces potential collection bias, as historical sampling may not have been perfectly random across all size classes or elevations. Second, spatial precision varied across the dataset; while modern specimens included exact GPS coordinates, older records often relied on county-level locations, which may introduce moderate error when paired with 4 km PRISM climate data. While temperature and precipitation were analyzed as possible drivers in this study, other important factors such as land-use change and pesticide exposure likely also contribute to the observed shifts in body size. The availability of bee species and sex also limited the number of bees measured, especially for males. In *B. pensylvanicus*, only 14 males were found and measured, leading to a limited analysis. Despite these constraints, the significant trends observed suggest that the environmental pressures of the last century are indeed leaving a measurable mark on pollinators and should be studied further.

Conclusion

This study demonstrates that the body size of Colorado's native bees has shifted significantly over the last century, driven by a combination of temporal, altitudinal, and climatic factors. While *B. pensylvanicus* and *A. texanus* are becoming smaller over time, *A. montana* is increasing in size, revealing that morphological responses to environmental change are genus or species specific. As climate change continues to alter the precipitation and temperature regimes of the Rocky Mountain region, understanding these morphological shifts will be critical for informing conservation strategies aimed at preserving the ecosystem services provided by these pollinators. Future research should investigate more specific phenological changes that may arise from these size changes to better predict long-term patterns in pollinators.

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