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Dimensions of Difference: Multi-Scale Consequences of Trait Variation in Bumble Bees

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Jacquelyn Lee Fitzgerald

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## Abstract

Individual differences among organisms have profound effects on their ecology and evolution. Yet, individuals are often treated as functionally equivalent, particularly when considered in aggregate. When intraspecific variation is considered, we have traditionally relied on simplifying assumptions, treating organisms as interchangeable units or reducing their differences to simple relationships. While conceptually and mathematically tractable, these assumptions may obscure patterns that inhibit our ability to understand basic ecology and predict responses to change. In this dissertation, I investigate how and why individuals vary and how the consequences of that variation scales to higher-order processes, particularly under global change. I focus on an assemblage of subalpine bumble bees (*Bombus* spp.) in the Colorado Rocky Mountains, a group of morphologically moderate and ecologically important insect pollinators that are sensitive to environmental variation and exhibit a substantial range of body sizes across species and caste. Chapter 1 represents a synthetic review of the ecological drivers and consequences of body size variation in bumble bees, a core life history trait that has been observed to shift in response to global change, consistent with broader patterns across taxa. I integrate this understanding to

identify hypotheses on the role of body size variation in shaping bumble bee fitness and responses to climate and land use change. This work highlights the multidimensionality of trait variation and how a fuller understanding of the causal factors driving such variation enhances our capacity to predict species responses to environmental variation. In Chapter 2, I build on these findings to develop a novel approach to analyzing complex changes in intraspecific trait distributions. I focus on techniques for understanding how trait values are gained or lost at the distributional tails and how these changes reflect environmental filtering processes. I find that climate and resource variation strongly affect the distribution of bumble bee body size across multiple mathematical dimensions – mean, variance, skew, and kurtosis. I observed caste-specific distributional changes, suggesting demographic forces guiding trait shifts, which correspond to changes in diet generalization and phenological activity. In Chapter 3, I investigate patterns of trait variation at the individual level, considering how foraging-relevant traits scale with body size and integrate across the entire organism. Compared to other eusocial insects, bumble bees are remarkably similar in morphology, despite commonly overlapping in space, time, and life history. I find that relatively small differences in trait covariation have large consequences for species function, suggesting adaptive patterns of trait variation that may promote the co-occurrence of morphologically similar groups. Overall, my dissertation advances our conceptual understanding of intraspecific variation in ecology, revealing how fine-scale trait variation among individuals shapes life history and scales to influence population- and community-level responses to environmental variation.

“Every one of us is, in the cosmic perspective, precious.

In a hundred billion galaxies, you will not find another.”

– Carl Sagan

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### **Dedication**

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## Table of Contents

|           |                                                                                                                           |
|-----------|---------------------------------------------------------------------------------------------------------------------------|
| 1         | Title                                                                                                                     |
| 2 – 3     | Abstract                                                                                                                  |
| 5 – 6     | Acknowledgements                                                                                                          |
| 7         | Dedication                                                                                                                |
| 8         | Table of Contents                                                                                                         |
| 9 – 10    | List of Tables and Figures                                                                                                |
| 11 – 32   | Chapter 1 – <i>Ecological drivers and consequences of bumble bee body size variation</i>                                  |
| 33 – 40   | Chapter 2 – <i>Intraspecific body size variation across distributional moments reveals trait filtering processes</i>      |
| 52 – 68   | Chapter 3 – <i>How does morphological integration and trait scaling influence foraging specialization in bumble bees?</i> |
| 69 – 91   | Tables and Figures                                                                                                        |
| 92 – 117  | References                                                                                                                |
| 118       | Appendix: Supporting information from Chapter 1                                                                           |
| 119 – 121 | Appendix: Supporting information from Chapter 2                                                                           |
| 122 – 128 | Appendix: Supporting information from Chapter 3                                                                           |

## List of Tables and Figures

### CHAPTER 1

- 68    **Table 1.1** – Studies considering environmental drivers or ecological consequences of  
bumble bee body size variation, analyzed within-species, between-species, or from both  
perspectives.
- 69    **Figure 1.1** - Photographs of bumble bee size variation within and between castes  
intraspecifically, and between species.
- 70    **Figure 1.2** - Summary of research on bumble bee body size: (A) Temporal trends in the  
number of studies, (B) studies categorized by drivers, consequences, and organizational  
level (intraspecific, interspecific, or both), and (C) specific drivers and consequences of  
size variation.
- 71    **Figure 1.3** – Diagram of the bumble bee colony life cycle
- 72    **Figure 1.4** - Diagram of hypothetical pathways by which bumble bee body size might  
shift as a consequence of: (A) increased climate temperatures, and (B) increased habitat  
fragmentation

### CHAPTER 2

- 74    **Box 2.1** – Conceptual diagram of trait distributional dimension (mean, variance, skew,  
kurtosis), simple and complex shifts in these dimensions, and how these shifts may  
reflect environmental filtering of intraspecific trait values.
- 76    **Figure 2.1** – Histogram of bumble bee body sizes across species and caste.
- 78    **Figure 2.2** – Plot of global model effects of climate and floral resources on bumble bee  
body size distributions, and the effects of body size distributions on bumble bee diet  
breadth and phenological activity.

- 80 **Figure 2.3** – Plot of the conditional model effects of snowmelt timing on the body size distribution of bumble bee queens across all species.
- 82 **Figure 2.4** – Summary plot of the conditional model effects of climate and floral resources on bumble bee body size distributions across all species and castes.
- 83 **Figure 2.5** – Summary plot of the conditional model effects of bumble bee body size distributions on diet breadth and phenological activity across all species and castes.

### CHAPTER 3

- 85 **Figure 3.1** – Conceptual outline of trait scaling and integration quantification approach.
- 87 **Figure 3.2** – Plot of allometric scaling relationships between bumble bee body size and head width.
- 89 **Figure 3.3** – Plot of the model effect sizes of the relationships between trait covariance and mean body size across bumble bee castes.
- 90 **Figure 3.4** – Plot of the model effect sizes of the relationships between trait covariance and diet breadth across bumble bee castes.

## CHAPTER 1

Ecological drivers and consequences of bumble bee body size variation

## Abstract

Body size is arguably one of the most important traits influencing the physiology and ecology of animals. Shifts in animal body size have been observed in response to climate change, including in bumble bees (*Bombus* spp.). Bumble bee size shifts have occurred concurrently with the precipitous population declines of several species, which appear to be related, in part, to their size. Body size variation is central to the ecology of bumble bees, from their social organization to the pollination services they provide to plants. If bumble bee size is shifted or constrained, there may be consequences for the pollination services they provide and for our ability to predict their responses to global change. Yet, there are still many aspects of the breadth and role of bumble bee body size variation that require more study. To this end, we review the current evidence of the ecological drivers of size variation in bumble bees and the consequences of that variation on bumble bee fitness, foraging, and species interactions. In total we review: (1) the proximate determinants and physiological consequences of size variation in bumble bees; (2) the environmental drivers and ecological consequences of size variation; and (3) synthesize our understanding of size variation in predicting how bumble bees will respond to future changes in climate and land use. As global change intensifies, a better understanding of the factors influencing the size distributions of bumble bees, and the consequences of those distributions, will allow us to better predict future responses of these pollinators.

## Introduction

Organismal body size is correlated with everything from individual thermoregulation and nutritional needs to population density and competition (Calder 1996). Body size influences how an animal interacts with its environment and other organisms, and ultimately its fitness, and an animal's body size itself can be determined by its environment and interactions with other organisms (Peters and Peters 1986). Body size variation is therefore an important component of predicting species responses to ongoing and increasing global change, especially for species key to ecosystem functioning, such as bees.

Among bees, bumble bees (*Bombus* spp. [Hymenoptera: Apidae]) exhibit substantial size variation within and between species (Michener 2000). Bumble bees are large and eusocial, with distinct castes that differ in both average size and in the amount of size variation (Medler 1962) (Figure 1.1). Within a single colony, *Bombus impatiens* worker size may vary by a factor of ten (an order of magnitude, Couvillon et al. 2010b), while workers of other, non-*Bombus*, eusocial bee species may only vary by a factor of two (Roulston 2000). With more than 260 species globally, bumble bees are abundant, generalist pollinators in natural and agricultural ecosystems, native to all continents except Antarctica and Australia (Goulson 2010). While they are found across a range of ecosystems, bumble bees are largely cold-adapted and occur in montane habitats. Bumble bees' large body size contributes to their success in these colder regions (Bishop and Armbruster 1999, Peat et al. 2005b), and their large size also appears to increase their sensitivity to climatic warming (Williams et al. 2009, Bartomeus et al. 2013).

Shifts in bumble bee body size have been recently observed (Gérard et al. 2020, Gérard et al. 2021), including decreases in average size (Oliveira et al. 2016, Nooten and Rehan 2020, Theodorou et al. 2020a), consistent with broader trends of declining animal body size with climate change (Gardner et al. 2011, Sheridan and Bickford 2011). The drivers and consequences of variation in bumble bee body size are multifaceted, making it challenging to predict the effects of these size distribution shifts. Disentangling the factors related to bumble bee size variation is particularly important considering recent bumble bee population declines and range shifts and their position as ecologically and economically important insect pollinators (Potts et al. 2010, Cameron et al. 2011, Cameron and Sadd 2020, Soroye et al. 2020).

Here, we review the current evidence of ecological drivers and consequences of body size variation in bumble bees. We define *ecological drivers* as determinants of body size variation — any natural or anthropogenic factors that directly or indirectly cause changes in size distributions. We define *ecological consequences* as the role of size variation — how size variation relates to fitness, foraging, and various species interactions. We first consider the role of sociality in bumble bee body size, then review

the proximate determinants of size variation, and biogeographic and climatic patterns of size variation in bumble bees. We then review the consequences of size variation on bumble bee physiology, pollination services, and interactions with other species. Finally, we identify hypotheses on the role of body size variation on bumble bees' fitness and population declines, particularly in the context of ongoing and increasing global change.

## Literature review

To identify and synthesize articles on the ecological drivers and consequences of bumble bee body size variation, we conducted a systematic literature search. We used the following search criteria in Web of Science, applied to titles, abstracts, and author keywords: (bombus OR “bumble bee” OR bumblebee) AND (“body size” OR “size variation”). We included papers published either online via early access or with a publication date before 31 December 2021. These parameters returned 304 papers. We then repeated these search parameters in Scopus, which returned 225 papers. We combined these two searches for a total of 350 papers. We then assessed whether each of these papers: (1) included bumble bees in their study; (2) described a cause or consequence of size variation (i.e., we excluded papers that only documented size variation); and (3) were ecological in nature (i.e., we excluded papers focused on molecular physiology or genetic mechanisms of size regulation). The genetic, physiological, and cellular mechanisms that regulate bee body size are important and have been reviewed elsewhere (Chole et al. 2019). We additionally included 36 relevant papers that we encountered but were not represented in our systematic searches (e.g., papers from older journals whose abstracts are not fully digitized, papers cited in articles included in our systematic search).

A total of 187 papers met our final criteria for inclusion, spanning 1955 to 2021 (Figure 1.2A, Table 1.1, Table S1.1). The number of papers focusing on bumble bee body size variation has steadily increased, peaking in 2021. From these, we categorized 67 papers as *drivers* and 134 as *consequences* (Figure 1.2B). Of these studies, 90 (48.6%) were conducted in or included bees from North America, 82

(43.9%) were conducted in or included bees from Europe, 13 (7.0%) in Asia, and 9 (4.9%) in South America. In total, 153 *Bombus* species were represented in these papers: *B. terrestris* was a focal species in 91 (48.6%) studies and *B. impatiens* in 53 (28.6%), while 58 species were only represented once. Overall, most papers focused on two easily reared species in temperate regions (*B. terrestris* and *B. impatiens*, 141 studies [76.2%]).

### **Size variation and sociality in bumble bees**

To understand the importance of bumble bee body size variation, we must first consider the role of size polymorphisms in the organization of bumble bee colonies. Bumble bees are eusocial hymenopteran insects with three distinct castes: large reproductive queens, smaller functionally sterile female workers, and similarly small males (Fletcher and Ross 1985) (Figure 1.1). The worker caste is the most variable in size, spanning up to an order of magnitude: for example, *B. terrestris* workers from a single colony can range from 0.05 to 0.40 g in mass (Goulson 2003). However, apart from the few commercially reared species (e.g., *B. impatiens* and *B. terrestris*), the degree of intraspecific size variation in bumble bees remains poorly understood, particularly in natural populations.

Bumble bee workers of different sizes tend to perform different tasks within the colony (Robinson 1992, Walton et al. 2019): larger workers are more likely to forage and guard the nest, whereas smaller workers are more likely to stay inside the nest to tend to the brood. Physiological differences in size, such as size-based circadian rhythms (Yerushalmi et al. 2006), are hypothesized to drive these labor divisions. While size-driven task differentiation can be flexible (Cartar 1992), even when size variation has been artificially reduced, larger workers are still more likely to forage than smaller workers (Crall et al. 2018, Holland et al. 2021). Thus, size-based task specialization is important to the social organization of bumble bee colonies, as is the flexibility of worker behavior in the nest (*but see* Foster et al. 2004, Jandt et al. 2009).

## **Ecological *drivers* of bumble bee body size variation**

### *Proximate determinants of size variation.*

The adult body size of bumble bees is determined during larval development and is shaped by larval diet and environment, mediated by interactions within the colony. As the temperature experienced by the brood increases, bumble bee adult body size tends to decrease (Guiraud et al. 2021, *but see* Kelemen and Dornhaus 2018), consistent with the “Temperature-Size Rule” (Atkinson 1996, Kingsolver and Huey 2008). Through regulation of nest temperature, humidity, and CO<sub>2</sub> levels (Vogt 1986, Weidenmüller et al. 2002, Heinrich 2004), bumble bee colonies are hypothesized to reduce variation in larval size driven by external environmental fluctuations. Bumble bee larval size is additionally controlled by diet, which is managed by tending workers. Brood that are fed larger volumes of pollen develop into larger adults (Pendrel and Plowright 1981), as are brood that are fed more frequently (Shpigler et al. 2013), and those that receive pollen with higher protein content (Rotheray et al. 2017). How much food a bumble bee larvae receives is shaped by how a species provisions its brood, either as “pollen-storers” that feed larvae individually or “pocket-makers” which feed larvae in groups (Sladen 1912). The position of larvae in pocket-making species affects how much food an individual receives, and larvae of species with this feeding strategy may be more variable in size (Hagen and Dupont 2013). In addition, larvae positioned closer to the center of the nest tend to be fed more frequently and experience a more stable thermal environment, and are generally larger than larvae on the periphery of the nest (Couvillon and Dornhaus 2009).

Larval size variation is also shaped by social dynamics within the colony. Early in the colony lifecycle, brood are primarily cared for by the queen (Goulson 2003) (Figure 1.3). As the colony develops, larvae are increasingly tended to by workers and average larvae size tends to increase as a consequence of improved brood care (Knee and Medler 1965, Shpigler et al. 2013), and appears to be unrelated to the size of the tending workers (Cnaani and Hefetz 1994). During early stages of the colony, queens may intentionally rear smaller workers to encourage worker sterility (Shpigler et al. 2013, Costa et

al. 2021). In some scenarios, large, dominant workers develop (Ayasse et al. 1995, Princen et al. 2020) and begin to lay haploid eggs, which are only able to develop into male bees (Free 1955a, Zhao et al. 2021b). Thus, queens may try to prevent usurpation of the colony by suppressing worker size, as predicted by the maternal manipulation hypothesis (Brand and Chapuisat 2012, Jandt et al. 2017).

### *The role of climate conditions on size variation*

Climate conditions are hypothesized to be a key driver of bumble bee body size. The relatively large size of bumble bees compared to other bees has contributed to their success in colder regions (Bishop and Armbruster 1999, Goulson 2003), but bumble bees can be quite flexible in their habitat requirements, such as the large, desert dwelling *Bombus sonorus* (Williams et al. 2014) and the smaller, neotropical *B. atratus* (Cameron and Jost 1998). Some species occur over broad climatic ranges, like the moderately-sized *B. griseocollis*, which can be found from the Southeastern USA to Northwestern Canada (Mitchell 1960), while others are more tightly constrained, like the large *B. polaris* and *B. alpinus*, which are exclusively found above the arctic circle and in the European alpine, respectively (Biella 2015, Williams et al. 2019). Thus, colder temperatures may limit the lower size range of bumble bees, but higher temperatures may not constrain upper limits, at least on evolutionary scales (Peat et al. 2005b, Ramírez-Delgado et al. 2016).

Thermodynamically, body size limits bumble bees at both ends of the thermal spectrum, such that larger bees appear to be more sensitive to high temperatures and smaller bees to low temperatures (Pyke 1978, *but see* Martinet et al. 2020). With increasing body size, bumble bees have a relatively smaller surface area to volume ratio and slower convective heat loss, while smaller individuals have a larger surface area to volume ratio, allowing for faster cooling (Heinrich 1983). Too hot, and these cold-adapted bees will experience heat stress and may ultimately die (Oyen and Dillon 2018). Too cold, and bumble bee flight muscles cannot contract quickly enough for flight (Stone and Willmer 1989). Consistent with Bergmann's rule (Bergmann 1848), bumble bee species and populations in colder climates tend to be

larger than those in temperate regions (Scriven et al. 2016, Gérard et al. 2018) but not necessarily males, (Cueva del Castillo et al. 2015). This sets up the general hypothesis that larger sized bumble bees may struggle to a greater degree with increasing temperatures associated with climate change (Bartomeus et al. 2013).

*The role of variation in floral food resources on bumble bee size*

The availability of floral food resources has strong influence over bumble bee body size because it determines the development of larval bees. Such effects depend not only on the quantity but also the quality of floral food resources. In general, access to abundant and high-quality floral resources supports greater mean size at the colony level (Grass et al. 2021). At the population level, with increasing food availability, bumble bees tend to produce larger workers and males (but not necessarily larger queens, Sutcliffe and Plowright 1988, Schmid-Hempel and Schmid-Hempel 1998, Kerr et al. 2021, Zaragoza-Trello et al. 2021). Larvae fed pollen with higher protein content tend to be larger in size (Tasei and Aupinel 2008, *but see* Vanderplanck et al. 2014), consistent with work in non-*Bombus* bee species (Roulston and Cane 2002). At the community level, greater floral diversity and number of native plant species appears to supports larger bodied bee species (Wray et al. 2014).

If bumble bee colonies experience resource limitation (i.e., an absence of abundant, high-quality floral food resources), then they may tradeoff between investing in fewer, larger workers and more, but smaller workers. Larger workers tend to be more efficient foragers (*see consequences for bumble bee foraging below*) but are more energetically expensive to produce (Smith and Fretwell 1974, Kerr et al. 2019). With limited resources, colonies may produce a greater number of smaller workers, which may return fewer resources to the colony but require fewer resources to produce. However, direct tests of how floral resource availability affects the resource allocation strategy of bumble bee colonies are needed and it is unclear which strategy (many small workers versus fewer large workers) confers a greater overall fitness benefit under different conditions. For example, under experimental conditions, when given access

to a greater abundance of resources, colonies of *B. vosnesenskii* (a medium-sized species) appear to favor producing fewer, larger workers, particularly during the early stages of colony development (Malfi et al. 2019, Kerr et al. 2021).

In the early stages of development, bumble bee colonies have few bees and may experience harsh environmental conditions (Figure 1.3) and are therefore more vulnerable to failure and may be particularly sensitive to the availability of floral resources. Nevertheless, life history theory suggests producing smaller offspring may be advantageous when energetic costs are high (Smith and Fretwell 1974), and it remains unclear the extent to which the production of fewer larger workers is a general pattern across species. Certain abiotic and biotic conditions may give rise to colonies preferentially producing a greater frequency of smaller bodied workers, and some species may generally adopt one strategy, but this is an outstanding question, particularly in wild systems.

#### *The role of competition on bumble bee body size*

Competition with other pollinator species may influence the body size distribution of bumble bees, and body size plays a key role in competitive interactions with other bumble bees (*see consequences for competition below*). The effect of competition on bumble bee body size is likely mediated through competition for floral resources. Competitively dominant species may deplete the availability of floral food resources and these decreases may in turn reduce the body size of other co-occurring bumble bees (Bowers 1985). With less and/or lower quality food available for developing brood, larvae will develop into smaller adult bumble bees. Alternatively, resource limitation as a result of interspecific competition may also force bumble bee colonies to send a greater number of workers out to forage. These workers may be smaller individuals that would otherwise remain in the colony tending brood, thereby reducing the average size of foragers. Smaller foraging workers also tend to be less productive foragers (*see consequences for foraging below*), which may reduce the overall quality of the colony's resource return.

This in turn may further reduce larval size and additionally reduce the quality of brood care if there are fewer nurses in the nest.

However, few studies have empirically asked how native *Bombus* species affect the size distributions of co-occurring bumble bee species (*but see* Bowers 1985), which limits our understanding of the mechanisms driving the coexistence of bumble bee species. Competition with managed honey bees (*Apis mellifera*) has been associated with decreased body size of native bumble bee species (Goulson and Sparrow 2009, Elbgami et al. 2014). It is probable that introduced bumble bee species influence the body size distributions of native bumble bees, as introduced *Bombus* species can compete with other bumble bees (Ings et al. 2006) and have been implicated in the decline of native bumble bees (Morales et al. 2013). The introduction of *B. terrestris* does not appear to have influenced the size of native bumble bees in Japan (Nagamitsu et al. 2006, Nagamitsu et al. 2010), but the effect of competition with introduced bumble bees on the body size of native *Bombus* species is an open question in other regions.

### **Ecological consequences of variation in bumble bee body size**

#### *Consequences of body size variation for bumble bee physiology*

The physiology of bumble bees varies with body size in ways that affect their interactions with the environment and other organisms. These ecophysiological differences do not necessarily scale linearly with size. For example, larger workers generally have larger eyes (Maebe et al. 2013, Kelber and Somanathan 2019), greater optical sensitivity (Streinzer and Spaethe 2014, Taylor et al. 2019), and stronger phototaxis response (Merling et al. 2020). For *B. terrestris*, with an approximate one third increase in body size, worker vision sensitivity and resolution doubles (Spaethe and Chittka 2003), and with an approximate doubling in body size, worker sensitivity to odors increases by 36-times (Spaethe et al. 2007). Higher visual and olfactory acuity may allow larger workers to better orient to, and differentiate between, floral resources in the landscape under a wider range of environmental conditions (Kapustjanskij et al. 2007). Larger individual workers also appear to learn tasks and make inferences faster (Worden et

al. 2005, Raine and Chittka 2008, *but see* Riveros and Gronenberg 2009, Evans and Raine 2014), which may improve their foraging abilities when presented with novel species or floral morphologies.

From a thermoregulation perspective, larger bumble bees tend to be better at maintaining consistent internal body temperatures at both the inter- and intraspecific levels (Heinrich 1983, Bishop and Armbruster 1999, *but see* Kelemen and Dornhaus 2018). Critically, however, the relationship between bumble bee size and thermal tolerance is less resolved. Of the studies that explicitly address the role of size on bumble bee critical thermal tolerance – the extreme limits of temperature an organism can tolerate – results are mixed. Some evidence finds that larger bumble bee workers, both between and within species, can tolerate more extreme heat and cold (Oyen et al. 2016, Oyen et al. 2021), whereas others find no effect of size on the thermal tolerance of workers (Hamblin et al. 2017, Oyen and Dillon 2018, Maebe et al. 2021), or in males (Martinet et al. 2020, Zambra et al. 2020). One important caveat is that the breadth of sizes considered in these studies is relatively small and may not fully capture the true range of sizes possible within a colony or population (*but see* Martinet et al. 2020). The relationship between thermal tolerance and bumble bee body size may be particularly important in the context of rising global temperatures, and this lack of resolution represents a considerable knowledge gap in our understanding of how bumble bee species may respond to climate change.

Larger body size may confer benefits in resource-rich environments, but larger bumble bee workers and queens may also be more vulnerable to resource limitation. For instance, larger workers have relatively less lipid stores compared to smaller workers (Couvillon et al. 2011), and may therefore be more vulnerable to starvation (Couvillon and Dornhaus 2010). In addition, there is no evidence that size affects bumble bee immune responses (Schmid-Hempel and Schmid-Hempel 1998, Baeuerle et al. 2020). Taken together, through improved thermoregulatory ability, learning capacity, and sensory sensitivity, larger individual bumble bees may be able to effectively forage under a greater range of environmental conditions, but larger body size is not universally beneficial.

*Consequences of body size variation for bumble bee foraging*

Body size influences bumble bees' ability to move between floral resource patches and to effectively collect pollen and nectar from flowers. Larger bee species, including bumble bees, tend to have larger maximum foraging ranges (Greenleaf et al. 2007, Mola et al. 2020), and relatively small differences in size between bumble bee species can translate to tenfold differences in potential foraging ranges (Westphal et al. 2006). Furthermore, larger bumble bee individuals can traverse greater distances at higher speeds (Ohashi et al. 2008), forage at different times of day and at lower light levels (Hall et al. 2021), and forage on lower density resource patches that may not be worth the energy expenditure for smaller bees (Foster and Cartar 2011).

Bumble bee body size also mediates an individual's floral choice and ability to extract pollen and nectar from flowers within a resource patch (Morse 1978, Barrow and Pickard 1984, Suzuki et al. 2007). Larger-bodied bees appear to forage for nectar from flowers with deeper corollas, whereas smaller-bodied bees prefer to forage from shallower or dish-shaped flowers, largely due to differences in tongue length (Peat et al. 2005a, Inoue and Yokoyama 2006, Liang et al. 2021). At the species level, longer-tongued (and larger-bodied) bumble bee species tend to have more specialized diets than shorter-tongued (and smaller-bodied) species (Wood et al. 2021). In addition, larger bumble bees tend to have higher foraging rates (Spaethe and Weidenmüller 2002, Ings 2005, Peat and Goulson 2005). Thus, larger workers generally return relatively larger pollen and nectar loads to the colony (Free 1955b, Ings et al. 2005, Kerr et al. 2019), and this may in part account for their greater metabolic needs (Plowright et al. 1993), which may increase the overall caloric needs of the colony (Cueva del Castillo et al. 2015, Hendriksma et al. 2019, Balfour et al. 2021).

Morphological size matching among plants and pollinators is an important component of plant fitness (Raine and Chittka 2005, Vázquez et al. 2009, Kuriya et al. 2015), and larger bumble bees may be more efficient at extracting pollen from some plant species (Klein et al. 2017, Koski et al. 2018). These larger bees remove and deposit more grains of pollen per visit than smaller bees both across species

(Willmer and Finlayson 2014, Földesi et al. 2021) and within species (Goulson et al. 2002, Russell et al. 2021), although this pattern may largely be due to larger bees' increased surface area (Thomson 1986). Depending on the size and morphology of a flower, smaller bumble bees may be more efficient pollinators, especially for complex floral morphologies (Stout 2000, Edens-Meier et al. 2011). For flowers that require buzz pollination, larger bumble bees can sonicate anthers at higher amplitudes and frequencies, releasing more grains of pollen (De Luca et al. 2014, Miller-Struttmann et al. 2017, De Luca et al. 2019, *but see* Arroyo-Correa et al. 2019, Rosi-Denadai et al. 2020).

The relative benefits of large workers to the colony are likely dependent on the type of floral resources available in a local ecosystem, and these benefits may change across the growing season as the number and variety of available floral species changes (e.g., Simanonok and Burkle 2014, CaraDonna and Waser 2020). Larger workers may offset their high rearing cost through greater resource return (Goulson et al. 2002), but once production costs are accounted for, smaller workers may provide equivalent or greater resource contributions (*but see* Kerr et al. 2019). The optimal range of forager sizes may then vary by local floral resource conditions, at different times of the year, and the density of competitors for resources (Goulson 2003). The distribution of bumble bee body sizes within a colony or population will mediate the number and diversity of resources in their diet and changes in bumble bee size distributions at the community, population, or colony level may have large consequences for foraging and pollination services.

#### *Consequences of body size variation for antagonistic interactions: Competition*

The influence of bumble bee body size on intra- and interspecific competition is complex as it integrates a variety of size related factors, including tongue length, phenology, and metabolism – all of which may be difficult to disentangle. For example, differences in phenology between bumble bee species has been observed to suppress the size of later emerging species, likely because earlier emerging species competitively dominate floral resources (Bowers 1985). In addition, because bee species with longer

tongues tend to be larger bodied (Cariveau et al. 2016, Arbetman et al. 2017), they may extract resources from flowers that are not be available to other bees (Harder 1986, Peat et al. 2005a). In other words, larger bodied species may be able to exploit a disproportionate share of high quality resources under resource rich conditions, but under poor resource conditions, smaller species may be advantaged by their lower metabolic costs (Pyke 1978).

At the community-level, tongue length, and by extension body size, may at least partly mediate coexistence between broad functional groups of bumble bees: species with relatively long, medium, or short-tongues (Inouye 1978, Pyke 1982, Ranta 1984). If species with similar tongue lengths are using the same floral resources, then competition between them should be strong, particularly when resources are limited. However, empirical evidence for competition among species with similar tongue lengths is generally lacking (Ranta and Vepsäläinen 1981, Ranta and Tiainen 1982, Goulson 2010). For example, honey bees (*Apis mellifera*) are a relatively short-tongued species, but their presence has been associated with decreased size of co-occurring bumble bee species of all tongue-lengths (Goulson and Sparrow 2009, Elbgami et al. 2014).

Body size likely contributes to competition within bumble bee species, both between conspecific foundress queens and between foragers from different colonies. Within an individual colony, larger workers tend to be more aggressive and dominant over other workers (van Doorn 1989, Pandey et al. 2020, *but see* Foster et al. 2004). However, to our knowledge no studies have explicitly addressed the consequences of size variation on intraspecific competition, which is a critical component for understanding the potential for species coexistence (Chesson 2000).

#### *Consequences of body size variation for antagonistic interactions: Predation*

The relationship between bumble bee body size and predation is relatively understudied, but evidence suggests that body size effects predator avoidance behavior. Across species, field evidence suggest that larger bumble bee species exhibit less anti-spider behavior (i.e., predator avoidance) than smaller-bodied

species (Dukas and Morse 2003). On an intraspecific level, larger *B. terrestris* foragers may also be better at avoiding predation by spiders (Gavini et al. 2020); however, this pattern may vary by species, as no evidence of sized-based differences in predator avoidance have been observed in *B. impatiens* (Jones and Dornhaus 2011). It is important to note that these two studies considered bumble bee behavior under laboratory conditions with simulated attacks or artificial spiders. Between species, larger bees' greater mass may allow them to escape predators more easily, whereas differences in behavior within species may indicate that larger workers initiate anti-predator behavior sooner. This may be because larger bumble bees tend to be less agile than smaller individuals, or that the greater visual acuity of larger bumble bees may allow them to detect potential predators faster than smaller bees. Larger bees may also be more obvious targets for attack. Size may mediate bumble bee vulnerability to non-spider predators, e.g., beewolves (*Philanthus* spp.), sphecid wasps (Sphecidae), birds, etc., but to our knowledge there are no studies that consider these relationships.

#### *Consequences for antagonistic interactions: Parasitism*

The size of bumble bee hosts may mediate the likelihood and intensity of parasite infection, which has been implicated in bumble bee population declines (Cameron and Sadd 2020). Bumble bees are commonly parasitized by the larvae of conopid (Conopidae) and phorid flies (*Apocephalus borealis*), in addition to tracheal mites (*Locustacarus buchneri*), intestinal parasites (*Crithidia bombi* and *Vairimorpha bombi*), and wax moths (*Aphomia sociella*), a European nest parasite. If larger host size allows for more physical space and opportunity for parasites to exploit (Kuris et al. 1980), then larger bumble bees may experience higher rates of parasitism. At an assemblage level, parasite richness may be higher for larger bees, at least in agricultural settings (Cohen et al. 2021), but across wild bumble bee species, there is no evidence that body size affects the diversity of associated parasitic species (Durrer and Schmid-Hempel 1995). However, larger bumble bee species and individuals do tend to have greater rates of conopid fly parasitism, both in wild communities (Muller et al. 1996, Schmid-Hempel and Schmid-Hempel 1996,

Otterstatter 2004, Malfi and Roulston 2014), and in commercial *B. impatiens* colonies (Gillespie et al. 2015). This does not necessarily indicate host preference for larger bees but may instead suggest that smaller workers are simply better at avoiding fly attacks, or conopids are less likely to develop in smaller hosts, or that because larger workers spend more time foraging, they are more likely to be attacked.

The role of body size on intestinal parasite infection is unclear. While some studies find no relationship between intraspecific size variation and parasite infection (Colla et al. 2006, Otti and Schmid-Hempel 2007, Figueroa et al. 2021), other evidence is mixed (Malfi and Roulston 2014, Van Wyk et al. 2021). Laboratory experiments suggest that while smaller workers may have more intense infections, larger individual *B. impatiens* were nearly twice as likely to transmit the trypanosomatid parasite *Crithidia bombi* (Van Wyk et al. 2021). As *Crithidia* is spread through feces, larger bees may shed a greater volume of parasites, increasing the likelihood of transmission. Host size may also mediate disease transmission through behavior, rather than physiological differences in vulnerability. Larger bees are more likely to forage (*see above*) and may have more opportunity to expose uninfected bees. If larger bees experience greater rates of parasitism, then this may further stress species and population that are already vulnerable as a consequence of their size.

#### *Consequences of body size variation for bumble bee fitness*

The body size distributions within bumble bee colonies, populations, and communities have the potential to mediate colony fitness and population dynamics. The most advantageous size distribution may differ across space, time, and resource environments. Greater size variation among workers may allow colonies to forage more efficiently under a greater range of biotic and abiotic conditions. Alternatively, greater average size among workers may allow colonies to maximize the volume of resources returned, even under less-favorable conditions. Both hypotheses could hold true under different contexts and for different species. Empirical evidence suggests that as mean worker size increases, bumble bee colonies tend to produce more new queens (Herrmann et al. 2018), and the benefits of larger workers hold across

resource conditions (Kerr et al. 2021). Although bumble bee colonies may produce a greater variety of worker sizes in less-favorable conditions, these colonies with more worker size variation do not appear to produce more workers or reproductives (Kelemen et al. 2020). Thus, greater average worker size may confer the greatest fitness benefits.

If larger workers tend to have lower survival rates (Kelemen et al. 2019, Kerr et al. 2019) and tend to be less hardy against starvation (Couvillon and Dornhaus 2010), then a greater proportion of large workers may be less desirable when floral resources are lower in quality or quantity (*but see* Kelemen et al. 2020). High worker mortality is also associated with smaller new queens (Muller and Schmid-Hempel 1992). In general, new queens in the fall are more variable in size compared to queens that emerge in the spring, which tend to be larger on average (Owen 1988, Inoue 2011). Such evidence suggests that smaller queens may be less likely to survive overwintering, perhaps due to faster depletion of macronutrient stores, which may be an important aspect to bumble bee persistence under climate change (Holm 1972, Vesterlund et al. 2014, *but see* Cameron and Jost 1998). Yet, among queens that do survive winter, larger individuals are not necessarily more likely to successfully found nests (Muller and Schmid-Hempel 1992).

It remains unclear how worker size may influence the size of males, but larger males tend to be more reproductively successful, producing more sperm (Zhao et al. 2021a) and copulating faster (Amin et al. 2012). In eusocial hymenopterans, there is strong sexual size dimorphism, where males are virtually always smaller than queens. Under limited resources to produce reproductive bees, colonies may then invest in producing more larger, higher quality males, rather than expending more resources to produce large, high quality, but expensive, queens (e.g., Trivers and Willard 1973). Bumble bees may invest more in males when resources are limited (Bourke 1997, Pelletier and McNeil 2003), and a further understanding of the role of body size in sex ratios would clarify the resource allocation strategies of bumble bee reproduction.

It is important to note that the consequences of size on an individual-level do not necessarily translate to colony-level fitness. For example, greater interspecific size improves thermoregulatory ability in bumble bees (Bishop and Armbruster 1999) but experimentally reduced worker size variation does not influence colony-level thermoregulation of the nest (Jandt and Dornhaus 2014). In total, larger overall size of individuals in a colony generally confers fitness benefits but these benefits come at a metabolic cost. If resources are scarce or the colony is otherwise stressed, it may be disadvantageous for a colony to produce large workers, males, or new queens. Empirical tests of this hypothesis will be important, particularly in the context of bumble bee decline and increasing global change.

### **Effects of global change on bumble bee body size**

#### *Consequences of climatic warming for bumble bee body size*

Anthropogenic climate change has the potential to dramatically alter bumble bee size distributions directly through exposure to increasing temperatures and indirectly by altering floral resources (Figure 1.4A). As climate change progresses, organisms will experience both higher overall temperatures and an increasing frequency and intensity of extreme temperature events (Pachauri et al. 2014). For bumble bees, these scenarios may act synergistically to alter the development of bumble bee larvae and the activity of adult bees. Some work has shown that the size distribution of active *B. impatiens* foragers is unaffected by air temperatures (Couvillon et al. 2010a), however, the highest temperature foragers experienced in this study (36°C) does not reflect the severity of extreme heat waves. Under extremely high temperatures (>40°C), bumble bees begin to approach their critical thermal limits (Oyen and Dillon 2018), which will restrict the foraging activity of bumble bees (Kenna et al. 2021) and may ultimately be lethal.

Reductions in bumble bee body size have been observed in multiple species over the past century in Europe and North America, and appear to be related in part to rising temperatures (Oliveira et al. 2016, Nooten and Rehan 2020, Theodorou et al. 2020a, *but see* Gérard et al. 2020) , consistent with general patterns of declining animal body size with climate change (Gardner et al. 2011, Sheridan and Bickford

2011). Critically, the specific mechanisms of bumble bee size declines remain unclear (Figure 1.4A). If declining size is a plastic response, then higher temperatures may directly reduce the size of developing larvae, as per the “Temperature-Size Rule” (Atkinson 1996, Kingsolver and Huey 2008, CaraDonna et al. 2018), or indirectly by altering the size of developing larvae by reducing the quality or quantity of floral resources (Forrest 2015, Kuppler et al. 2021). If declining body size is an adaptive response, then higher temperatures may directly increase the mortality of large individual bumble bees, selecting for smaller adult size of queens and males (Leiva et al. 2019).

Although there have been no direct tests of the mechanism by which bumble bee populations have experienced size declines, laboratory evidence suggests that higher temperatures may decrease the size of developing larvae. Under standard ranges of bumble bee nest temperatures (20–30°C), the average size of bumble bee larvae does not vary with developmental temperature (Kelemen and Dornhaus 2018), perhaps because workers are able to cool the nest environment through wing fanning (Vogt 1986). However, higher temperatures (>30°C) may decrease the size of developing workers and males (Guiraud et al. 2021). Field evidence on the effect of greater temperatures on bumble bee size is mixed, with some evidence suggesting higher ambient temperatures drives smaller body size and more size variation in adult foragers (Theodorou et al. 2020b), while some finds that worker and queen size increases and size variation decreases, with increasing temperatures (Zaragoza-Trello et al. 2021). Regardless, larger overall bumble bee species appear to be disadvantaged under high temperatures (Osorio-Canadas et al. 2016, Gérard et al. 2021). Other extreme climatic events, such as drought, may also shape the body size distributions of bumble bees (Hung et al. 2021), but this is less explored. As climate change continues and accelerates, declines in bumble bee body size at the colony, population, or community-level may continue, and may have negative consequences for colony fitness and worker foraging abilities (*see above*) with cascading consequences on the plants that rely on bumble bees for pollination.

*Consequences of land use change for bumble bee body size*

Land use change is a complex process and there are multiple potential mechanisms underlying the effects on bumble bee body size. For example, habitat loss and fragmentation affect the dispersal ability of foragers and reproductives, which should *select* for larger body sizes. The loss of floral resources and urban heat island effects may alter the *development* of different sized bees, and exposure to insecticides may affect *which* sized bees survive. Thus, the effects of land use change on bumble bee body size variation are complex and understanding them requires a multi-faceted approach.

The conversion of natural areas to agricultural or urban uses, leading to the loss of floral resources and available nesting habitat, is the most direct consequence of land use change on bees (Winfree et al. 2011, Wray et al. 2014). Outside of these food and nesting losses, increasing intensity of land conversion increases the distance between resource patches and bee movement is subsequently restricted (Van Dyck and Matthysen 1999, Williams et al. 2010). Larger bumble bee species generally have larger foraging ranges (*see above*) and may be better able to traverse these distances, potentially leading to selection for larger body size (Figure 1.4B). Empirical evidence generally supports this idea: larger bumble bees are associated with greater landscape fragmentation at both interspecific (Hirsch et al. 2003, Williams et al. 2010, Jauker et al. 2012, Maas et al. 2021) and intraspecific levels (Murúa et al. 2011, Gérard et al. 2020). The effect of fragmentation on body size may depend on the relative mean size of species, with larger overall bumble bee species increasing in size and smaller species decreasing in size (Gérard et al. 2021).

Beyond simple losses of floral resources and nesting habitat, the landscape surrounding resource patches exerts a strong influence on bumble bee body size (Hirsch et al. 2003, Persson and Smith 2011, Jauker et al. 2012, Hutchinson et al. 2021). For example, conventional agricultural lands tend to support larger bee species at an interspecific level (likely for dispersal-related reasons, De Palma et al. 2015), but smaller average worker size on an intraspecific level (likely for nutrition-related reasons, Gayer et al. 2021). Urbanization has similarly complex effects, with evidence suggesting shifts in interspecific size-distributions in favor of large-bodied bee species at the community level (Bennett and Lovell 2019).

However, at the species level, the effects of urbanization are mixed, with evidence for both increases (Theodorou et al. 2020a) and decreases in size (Eggenberger et al. 2019). The specific effects of urbanization may be difficult to disentangle from modifications related to climate, including urban heat island effects (Hamblin et al. 2017), reduced floral food resources (Burdine and McCluney 2019), and toxic pesticide exposures (Siviter et al. 2021).

The interactive effects of pesticides can compound the effects of land use changes on bumble bee size. The timing, type, and relative intensity of pesticide exposure likely differs with the type of land use, i.e., exposure from conventional agricultural fields differs from that of urban yards. New generations pesticides, including neonicotinoids, which may be less harmful to vertebrates but act as neurotoxins to insects, have been found translocated to nectar and pollen, where they may be consumed by bumble bees and other pollinators (Blacquiere et al. 2012). Sufficiently intense pesticide exposures are lethal (Straw et al. 2021), and smaller bumble bees have lower lethal doses (Thompson 2001). Smaller species and individual bees may therefore be more vulnerable to mortality following pesticide exposure. Pesticides can also have sub-lethal effects on bumble bees, including impaired brood development, decreased foraging, and damage to the gut (Morandin et al. 2005, Straw and Brown 2021). The specific effects of exposure can vary by the type of pesticide (Bernauer et al. 2015, Siviter et al. 2021), which may also be body-size related.

### **Conclusions and future direction**

Body size variation in bumble bees is integral to the social organization of the colony and has strong effects on bumble bee foraging and fitness. Understanding the ecological drivers and consequences of bumble bee body size variation requires integration of ecology, evolution, and physiology, and can help us better predict the persistence of this key group of pollinators under global change. It is perhaps not surprising that the current evidence suggests that bumble bee body size represents an important, multidimensional trait that can strongly modify how these organisms respond to environmental changes.

If we are to better understand and predict the fates of bumble bee species under continued global change, body size is likely to play a key role.

However, considerable knowledge gaps remain in our understanding of the role of body size variation on bumble bee vulnerability to population decline. As a starting point, we still lack a basic understanding of body size distributions at the species level and how this variation integrates with other fundamental aspects of bumble bee ecology, including diet breadth, competition, and colony fitness. Furthermore, most work in this area focuses on a handful of species (e.g., *Bombus impatiens* and *B. terrestris*), mostly from temperate regions, and mostly under laboratory conditions. We have learned a great deal from these studies, but we understand much less about how size plays out in the wild under a range of environmental conditions and bumble bee species. To address this knowledge gap, observational studies of the size distribution of wild bumble bee populations conducted across time and space that can capture variation in climate and floral resources, and experiments that leverage understanding of this natural variation, would be valuable.

As global changes in climate and land use advance and intensify, it is likely that shifts in bumble bee body size distributions will also continue, and the direction and magnitude of these size shifts will have consequences for pollination services. A better understanding of the environmental variables that have a major influence on bumble bee body size distributions will have important implications for our ability to predict species responses to global change.

## CHAPTER 2

Intraspecific body size variation across distributional moments reveals trait filtering processes

## Abstract

1. Natural populations are composed of individuals that vary in their morphological traits, timing, and interactions. The distribution of a trait can be described by several dimensions, or mathematical moments – mean, variance, skew, and kurtosis. Shifts in the distribution of a trait across these moments in response to environmental variation can help to reveal which trait values are gained or lost, and consequently how trait filtering processes are altering populations.
2. To examine the role and drivers of intraspecific variation within a trait filtering framework, we investigate variation in body size among five wild bumble bee species in the Colorado Rocky Mountains. First, we examine the relationships between environmental factors (climate and floral food resources) and body size distributions across bumble bee social castes to identify demographic responses to environmental variation. Next, we examine changes in the moments of trait distributions to reveal potential mechanisms behind intraspecific shifts in body size. Finally, we examine how intraspecific body size variation is related to diet breadth and phenology.
3. We found that climate conditions have a strong effect on observed body size variation across all distributional moments, but the filtering mechanism varies by social caste. For example, with earlier spring snowmelt queens declined in mean size and became negatively skewed and more kurtotic. This suggests a skewed filter admitting a greater frequency of small individuals. With greater availability of floral food resources, queens increased in mean size, but workers and males decreased in size. Observed shifts in body size variation also correspond with variation in diet breadth and phenology. Populations with larger average body size were associated with more generalized foraging in workers of short-tongued species and increased specialization in longer-tongued workers. Altered phenological timing was associated with species- and caste-specific shifts in skew.

4. Across an assemblage of wild bumble bees, we find complex patterns of trait variation that may not have been captured if we had simply considered mean and variance. The four-moment approach we employ here provides holistic insight into intraspecific trait variation which may otherwise be overlooked and reveals potential underlying filtering processes driving such variation within populations.

## Introduction

Intraspecific trait variation is the raw material on which ecological and evolutionary processes act. The distribution of traits in a population can mediate intraspecific responses to biotic and abiotic factors (Levins 1968; Sultan 2000; Violle et al. 2007), and the traits of individuals in a population can be a result of environmental filtering (Diaz, Cabido & Casanoves 1998; Messier, McGill & Lechowicz 2010).

Understanding how intraspecific trait variation is influenced by environmental variation, and how it in turn affects species function (e.g., resource use and phenology), can help to advance our mechanistic understanding of ecological and evolutionary processes (Cianciaruso et al. 2009; Lajoie & Vellend 2015; Niu, Zhang & Lechowicz 2020).

Trait distributions can be described by multiple dimensions, or mathematical moments: mean, variance, skew, and kurtosis. Whereas mean and variance reflect the position and scale of a trait distribution, skewness reflects the asymmetry, and kurtosis the relative tailed-ness (Box 2.1). Deviations from the normal bell-shaped curve can be described through these higher moments (skewness and kurtosis). At the intraspecific level, shifts in one or more of these moments with environmental variation can reflect changing filters acting on phenotypic plasticity, local adaption, or a combination of these processes (Albert et al. 2010; Des Roches et al. 2018). In a simple example, with greater resource availability we might observe a straightforward increase in mean trait values, such as larger body size following a reaction norm, without changes in the spread or shape of the distribution. This might suggest

a filter towards larger trait values and against smaller values, a process we call directional filtering (Bulmer 1971; Endler 1986).

However, larger mean body size may also emerge from an increased frequency of larger individuals without a change in the range of trait values in a population. Such a shift would alter the shape of the trait distribution, making it more asymmetric and suggesting what we refer to as a skewed filter (Box 2.1). In contrast, a loss of the largest and smallest individuals would reduce variance and increase kurtosis, without necessarily a change in the mean. Such a pattern may indicate stabilizing filtering around a central trait value (Rolhauser & Pucheta 2017; Loranger et al. 2018). Multiple filtering scenarios may play out concurrently, such as a change in the mean trait value coupled with a loss of extreme individuals reducing variance and increasing kurtosis, suggesting both a directional and stabilizing filter (Le Bagousse-Pinguet et al. 2017; Gross et al. 2021).

Characterizing the correlations of higher moments of a distribution (variance, skewness, and kurtosis) with environmental variation allows us to consider the loss or addition of trait values at the distributional tails. These functionally rare traits may influence a population's capacity to adapt to future environmental variation and interspecific interaction patterns (Levins 1968; Ellers et al. 2012). Extreme trait values at the distributional tails may allow those individuals to exploit unique resource or phenological niches as compared to the rest of the population (i.e., the niche variation hypothesis; Van Valen 1965; Bolnick et al. 2007; Violle et al. 2017). However, under physiologically stressful conditions, such as a hotter climate, rare traits may be lost (Bradshaw & Hardwick 1989; Hoffmann & Merilä 1999), especially if they are metabolically demanding to develop or maintain (Kleiber 1947; Relyea 2002; Somjee et al. 2018); this would manifest in changes in the skewness and variance of the trait distribution (Parsons 1995; Cotton, Fowler & Pomiankowski 2004). Alternatively, greater trait variation may increase if harsh conditions promote risk-spreading within a population (Badyaev 2005).

Of an organism's many traits, body size is one of the most fundamental (Peters & Peters 1986; Calder 1996). The size of an individual has a strong influence on nearly every aspect of their life history,

including diet (Kleiber 1947), competitive ability (Brooks & Dodson 1965), and thermoregulation (Stevenson 1985). In addition, body size itself can be strongly influenced by resources and environmental conditions during development (Schmidt-Nielsen & Knut 1984; Smith & Lyons 2013). While all populations are comprised of individuals of varying body sizes, intraspecific size variation is especially striking in social insects, where reproductive and non-reproductive females are largely distinguished by size (Oster & Wilson 1978). Among some eusocial groups there is also substantial variation within castes, such as in bumble bees, where sister workers may vary in size by an order of magnitude (Medler 1962; Fletcher & Ross 1985; Goulson 2003; Fitzgerald, Ogilvie & CaraDonna 2022).

In bumble bees, social castes (queens, workers, and males) perform distinct functional roles, and therefore experience different ecological constraints on body size (Light 1942; Free 1955; Fitzgerald, Ogilvie & CaraDonna 2022). Consequently, the functional role of size variation differs among caste, and shifts in the body size distributions within and across caste may reflect demographic responses to variation in the environment (e.g., Ogilvie & CaraDonna 2022). For example, queens, the central reproductive unit of the colony, may be more likely to exhibit patterns indicative of stabilizing filters to ensure reproductive success (i.e., decreased variance, increased kurtosis), whereas workers, representing colony growth and responsible for most resource acquisition, may be filtered to adapt to shifting resource availability and increase risk spreading (i.e., increased skewness and variance) (Wilson 1971; Anderson 1984; Schmid-Hempel & Schmid-Hempel 1998). Males, as the developmentally cheaper reproductives, may be more likely to exhibit directional filtering to increase mating success (i.e., increased mean) (Amin, Bussière & Goulson 2012; Zhao et al. 2021).

To examine how variation in trait distributions correspond to biotic and abiotic variation, and potentially link to trait filtering processes, we investigate the environmental factors and ecological effects associated with intraspecific body size distributions in an assemblage of wild bumble bees in the Colorado Rocky Mountains, USA. We characterize changes in body size distributions across all moments (mean, variance, skew, kurtosis) at the population level and across social castes. Specifically, we ask: (1)

what is the relationship between body size distributions and climate and floral resource conditions? And (2), what are the effects of size variation on bumble bee resource use and phenology? We then use these trait distribution patterns to ask how they correspond to trait filtering processes and consider social caste to understand how demography may influence these processes. By examining all distributional moments, we move beyond simple mean trait relationships to consider how environmental processes shape other features of trait distributions including symmetry and extreme trait values. Moreover, our work advances our understanding of intraspecific variation within a trait filtering framework and highlights the usefulness of social species for addressing these questions within and among species.

## Materials and Methods

### *Study system*

We conducted our study of five wild bumble bee species in a series of high-elevation subalpine meadows near the Rocky Mountain Biological Laboratory (RMBL), in Gothic, Colorado, USA (2,900 m *a.s.l.*). The area is highly seasonal, typical of high-elevation and high-latitude regions, with a short growing season beginning with spring snowmelt (April-June) and ending as temperatures cool in the autumn (September-October) (CaraDonna, Iler & Inouye 2014; Cordes et al. 2020). We conducted our study in six established research sites in the East River Valley of the Elk Mountains (*for details see* Ogilvie & CaraDonna 2022). Each site is approximately 500 m in diameter and separated by at least 1 km. This scale reflects typical bumble bee foraging distances in the region (Elliott 2009; Geib, Strange & Galen 2015), and we observed no individuals travelling between sites across three years of mark-recapture surveys (unpublished data). Our research did not require animal ethics approval. We had permission to conduct field work in the Gunnison National Forest with a U.S. Department of Agriculture Forest Service Special Use Permit GUN1120 and on private land from the RMBL and the Town of Mt. Crested Butte.

### *Quantifying bumble bee body size and size variation*

During three growing seasons from 2020-2022, we conducted twice-weekly surveys of our study sites (41 weeks and 297 survey hours in total). We alternated visiting each site in the morning (9:00-12:00 h) and afternoon (13:00-17:00 h) to capture a range of foraging times and daily weather conditions. During each survey, we systematically searched a site for bumble bees and netted individuals for a minimum of 1 hour of active sampling effort. For each netted bee we recorded: (1) species identity, (2) caste (i.e., overwintered queen, worker, male), and (3) intertegular distance (ITD), the space between the wing bases (tegulae) and a common and robust proxy for overall bee body size (Cane 1987; Hagen & Dupont 2013). We identified bees to species in the field based on distinctive colour patterns following Williams et al. (2014) and against reference specimens in the RMBL Natural History Collection. Before releasing, we marked each bee with a paint pen to avoid remeasuring individuals.

We calculated the four moments of the body size distributions (mean, variance, skew, and kurtosis) separately for each species, caste, site, and year combination. We only made these calculations for species-caste combinations with sample sizes  $\geq 30$ . We considered body size variation as the robust coefficient of variation (RCR): the ratio of the interquartile range (IQR) to the median ( $RCV = \frac{IQR}{M}$ ). This measure of dispersion is less sensitive to outliers than parametric interval estimates, and thus better suited to characterize variance for skewed distributions (Arachchige, Prendergast & Staudte 2020). We

considered skewness as the Fisher-Pearson standardized third moment coefficient:  $\frac{\frac{\sum_{i=1}^n (x_i - \bar{x})^3}{n}}{\left(\frac{\sum_{i=1}^n (x_i - \bar{x})^2}{n}\right)^{3/2}}$ , where

values are unbounded and their sign represents the direction and magnitude of the asymmetry: negative (left skewed), positive (right skewed), or zero (symmetric). We considered kurtosis as Pearson's measure of kurtosis:  $\frac{n \cdot \sum_{i=1}^n (x_i - \bar{x})^4}{(\sum_{i=1}^n (x_i - \bar{x})^2)^2}$ , where excess kurtosis greater than zero represents a heavier-tailed distribution (leptokurtosis), less than zero represents lighter tails (platykurtosis), and equal to zero a normal distribution (mesokurtosis). To calculate skewness and kurtosis, we used functions from the R package

*moments* (Komsta & Novomestky 2015). Skewness and kurtosis are related through the inequality  $K \geq \beta S^2 + \alpha$ , such that an increase in skewness (i.e., greater trait asymmetry) will be accompanied by an increase in kurtosis (i.e., greater trait evenness) (Cullen & Frey 1999). In our data, skewness and kurtosis were only weakly correlated (adjusted  $R^2 = 0.02$ , Pearson correlation coefficient = 0.159; Figure S2.1 and Table S2.1).

### *Quantifying variation in climate*

We selected two climate variables known to influence bumble bee populations in our study system (Ogilvie & CaraDonna 2022): (1) the timing of spring snowmelt for overwintered queens and (2), the ratio of summer temperature to rainfall for workers and males. Queen emergence in the spring is correlated with snowmelt timing (unpublished data). For overwintered queens, the timing of snowmelt affects the duration that individuals spend in winter diapause. Earlier snowmelt is hypothesized to be favourable for winter survival, as shorter winters allow queens to spend less time in diapause depleting energy stores (Beekman, Van Stratum & Lingeman 1998), thus increasing their abundance in the spring (Ogilvie & CaraDonna 2022). Here, we defined snowmelt timing as the first day of bare ground. Using three HOBO pendant temperature/light loggers (Onset, part no. UA-002-64; Bourne, Massachusetts, USA) deployed year-round at each site, we detected bare ground as the average first day of year with air temperature  $> 5^{\circ}\text{C}$  and light  $> 10,000$  lux, a robust and common measure of spring onset in this snow-dominant subalpine system (e.g., Forrest & Thomson 2011).

For workers and males, summer climates are hypothesized to affect the activity and abundance of bees (Iserbyt & Rasmont 2012; Zaragoza-Trello et al. 2021; Ogilvie & CaraDonna 2022). Here, we use a ratio of mean daily maximum temperature to cumulative rainfall to account for the effect of precipitation (Ogilvie et al. 2017) in a single measure for greater interpretability (similar to Ogilvie & CaraDonna 2022). We measured temperature with the HOBO data loggers at each of our sites, and rainfall was measured daily at one central site with a standard US National Weather Service rain gauge by local

RMBL resident bumble bee. This ratio of temperature to rainfall represents a measure of climate variability between sites normalized by precipitation experienced at the level of valley. For workers, we used weather conditions in June and July, and for males we used conditions in July and August, a division that reflects the seasonal activity period of each caste. Higher ratios indicate hotter and drier conditions, which may be favourable to development if these conditions are within tolerable limits (Zaragoza-Trello et al. 2021; Ogilvie & CaraDonna 2022). However, exceptionally hot and dry conditions may negatively impact bee foraging and survival (Oyen, Giri & Dillon 2016; Oyen et al. 2021). In addition, bumble bees exhibit temperature-mediated body sized variation consistent with the temperature-size rule (Kelemen & Dornhaus 2018; Guiraud et al. 2021), where higher temperatures shorten the larval developmental period leading to smaller adults (Atkinson 1994; Kingsolver & Huey 2008).

#### *Quantifying variation in floral resources*

We conducted weekly surveys of floral abundance at each site, counting the abundance of flowers of plant species visited by bumble bees in 15 permanent 20 x 0.5 m belt transects distributed throughout each site (Ogilvie & CaraDonna 2022). For our analyses here, we summed floral abundance across transects and year at each site. We then scaled floral abundance by their visitation rank, represented as the sum of scaled floral abundance:  $\sum S_i = N_i (\frac{V_i}{V_{max}})$ , where  $S_i$  = scaled abundance of species  $i$ ,  $N_i$  = abundance of species  $i$ ,  $V_i$  = number of visits to species  $i$ , and  $V_{max}$  = number of visits to the most visited species. We used visitation data from the long-term bumble bee monitoring at our focal sites during our 2020-2022 study period (see Ogilvie & CaraDonna 2022). This scaling approach allowed us to prevent rarely visited but abundant floral species from representing an inappropriate share of the resource environment.

From these rescaled flower counts, we estimated the floral resources during the developmental period of bumble bee caste. For queens, which are born the previous year and overwinter as adults, we

considered total floral resources in the prior year ( $t - 1$ ). For workers and males, which develop and are active within a single season, we considered floral resources in the current year from the start of the season through the end of their activity period (August and September, respectively). For improved model convergence, we then standardized these counts by subtracting the mean and dividing by the standard deviation.

#### *Quantifying bumble bee resource use*

To assess the effects of body size variation on bumble bee resource use, we uniquely calculated diet breadth for each species from our long-term records for each caste, site, and year combination. We use standardized Hurlbert's niche breadth as our measure of diet breadth, which allowed us to account for, and scale variation in, resource availability (Hurlbert 1978). Hurlbert's niche breadth ( $B'$ ) is defined as:

$$B' = \frac{1}{\sum \left( p_j^2 / a_j \right)}$$

Where  $p_j$  = proportion of individuals using resource  $j$  and  $\sum p_j = 1$ , and  $a_j$  = the proportion of resource  $j$  to total resources ( $\sum a_j = 1$ ). To standardize  $B'$ , we use  $B'_a = \frac{B' - a_{min}}{1 - a_{min}}$ , where  $B'_a$  = standardized Hurlbert's niche breadth and  $a_{min}$  = the smallest observed proportion of all resources ( $\min a_j$ ). Values closer to one represent more generalized foraging, while values closer to 0 represent more specialized foraging.

#### *Quantifying bumble bee phenology*

To assess the effects of body size variation on bumble bee timing, we calculated two metrics of phenology for each species and caste: (1) emergence date and (2) activity period. Using weekly bumble bee census data from long-term monitoring in our sites (Ogilvie & CaraDonna 2022), we constructed kernel density estimates of daily abundance for every species and caste combination at each site in each

year. From each density estimate, we considered emergence date as the day of year on which 2.5% of the population had emerged and activity period as the number of days between emergence date and the date on which 50% of the population of each caste had emerged. We chose to represent emergence as the 2.5% mark as this measure is less sensitive to sample size than first sighting (CaraDonna, Iler & Inouye 2014), and activity period as the length of time between emergence and when half of the population is active as this metric captures peak activity of the bees in this system.

### *Data analysis*

We conducted all our analyses in R version 4.2.2 (R core team 2019), using a series of Bayesian mixed effects models with the package *brms* (Bürkner 2017). For environmental drivers of body size variation, we used Bayesian mixed effects models to estimate the fixed effects of climatic and floral resource conditions. We included species as a random effect to estimate species-specific intercepts and slopes, and modelled each caste (queen, worker, male) independently, as we hypothesized each caste would be most strongly affected by different climatic predictors and floral resources (*see above*). For the effects of body size variation, we analysed the fixed effects of each body size distribution moments on diet breadth, emergence timing, and activity period, modelling each caste separately using Bayesian mixed effects models as described above, with species as a random effect.

We modelled each moment (mean, variance, skew, and kurtosis) independently, each moment with their own weakly informative priors. For the mean, we defined the prior as a gamma distribution with a lower bound of zero and specified  $k$  and  $\theta$  to 2; for variance, we used a beta distribution bounded between 0 and 1 with  $\alpha = 2$  and  $\beta = 5$ ; for skewness and kurtosis, we used a normal distribution centered at zero with  $\sigma = 1$ . For effects on the moments, we defined the priors as the intercept, and for effects of the moments, we defined the priors as the slope. We employed three Markov chains, each run for 4,000 cycles with a 2,000-iteration warmup phase. To avoid divergent transitions after warmup, we adjusted the `adapt_delta` parameter to 0.99 to improve smoother sampling behavior and convergence of

the Markov chains. We assessed model convergence using the Gelman-Rubin statistic  $\hat{R}$  – all  $\hat{R}$  values were below 1.01. We evaluated the evidence for both global (average across all species) and conditional (species-specific) effects considering the 75<sup>th</sup>, 85<sup>th</sup>, and 95<sup>th</sup> credible intervals (CI). Higher moments (variance, skew, and kurtosis) are emergent properties of the population and therefore have a lower sample size than the mean ( $N = 18$ ), which we modelled from individual data. We chose to accept a more stringent degree of evidence for the first moment (mean) to account for the difference in sample size across moments. We consider strong evidence of a species-level effect if the posteriors do not cross zero at the 95<sup>th</sup> CI for the first moment (mean) and at the 85<sup>th</sup> CI for the higher moments (variance, skew, and kurtosis).

## Results

Over three years (2020, 2021, and 2022), we measured the body size of 2,456 individual bees from the five most common *Bombus* species in the area: *Bombus appositus* ( $N = 500$ , 20.4% of individuals), *B. bifarius* ( $N = 688$ , 28.0%), *B. flavifrons* ( $N = 750$ , 30.5%), *B. insularis* ( $N = 164$ , 6.7%), *B. rufocinctus* ( $N = 354$ , 14.4%) (Figure 2.1). During the study period, there was considerable variation in climate conditions spatially and temporally: across years, site-level snowmelt timing varied by nearly three weeks, spanning from 19 April to 8 May. Across years and sites, mean maximum daily summer temperatures ranged from 23.8°C to 35.4°C. Across years, total precipitation ranged from 27.68 – 98.04 mm, The ratio of these maximum temperatures to precipitation varied nearly 2-fold (0.38 – 0.71 °C:mm rainfall). Variation in floral resource abundance spanned nearly 10-fold across site and year, ranging from 30 to 291 flowers/m<sup>2</sup> (summed across each year).

### *How does size variation differ among castes and species?*

Within species, bumble bees exhibited a characteristic bimodal size distribution (Figure 2.1). Queens were, on average, 41.0% larger than workers and 35.6% larger than males. The distribution of male body

size was generally a subset of worker size. Within a caste, bumble bee body size was normally distributed with light tails (platykurtic) (Figure 2.1, S2.1). The robust coefficient of variation in body size ranged from 9.8% (*B. bifarius* males) to 18.7% (*B. flavifrons* workers), with workers exhibiting a higher degree of body size variation than the other castes. When considered in aggregate across space and time, body size distributions within species and caste were not strongly skewed. When considering how body size distributions varied between years and sites, distributions became more complex, often showing a high degree of skewness (both positive and negative) and variation in the degree of kurtosis (Figure S2.2).

*How does variation in climate and floral resources effect body size distributions?*

Climatic variation had strong and consistent conditional effects on mean bumble bee body size across caste and species, but with mixed effects on other moments (Figure 2.2). With earlier snowmelt, queens declined in mean size across species (Figure 2.3). This was accompanied with negative skewness and increased kurtosis (Table S2.2), suggesting that a decline in mean size was driven by an increasing frequency of small-bodied queens. For workers, hotter and drier mid-summer conditions were associated with larger mean worker body size across all species (Table S2.3). Variation in worker size declined under hotter and drier conditions, as well as kurtosis (Table S2.2). Under hotter and drier conditions, male body size increased, without strong effects on higher moments (Tables S2.2 and S2.3).

The abundance of floral food resources did not have consistent effects on body size across caste and species. For queens at the global level, greater floral abundance in the prior year was weakly associated with larger body size and increased variance, without evidence of an effect on higher moments (Figures 2.2, 2.3, and Table S2.4). At the conditional level, there were mixed effects across all moments and species. For example, *B. appositus* showed strong shifts across all moments with increasing floral resources, while *B. flavifrons* only showed a decrease in kurtosis (Figure 2.4). For workers, an increase in floral resources in the current year was strongly associated with smaller mean size and increased variance across all species, without evidence of an effect on variance and skewness across species, except for

increased kurtosis in *B. flavifrons* (Tables S2.4 and S2.5). For males, increasing floral abundance was strongly associated with declining mean size and increased variance at the global and conditional levels, without changes in the other dimensions of the body size distributions (Table S2.4 and S2.5).

*Is body size variation related to resource use and phenology?*

Shifts in mean body size were associated with variable changes in resource use across caste at the global level (Table S2.6). For queens, larger body size and higher variance was correlated with increased diet breadth in queens at the global level, without effects of skewness or kurtosis on resource use (Table S2.6). At the species level, there were strong positive effects (i.e., increased generalization) of mean size on diet breadth in *B. insularis* and strong positive effects of body size variance in *B. appositus*, *B. insularis*, and *B. bifarius* (Table S2.7). In workers and males, larger body size and higher variance were strongly correlated with greater diet breadth at the global level (Table S2.6). At the conditional level, there were mixed and inconsistent effects across species and moments (Table S2.7). There is strong evidence that *Bombus rufocinctus* workers and males foraged more generally with increasing mean body size, while *B. appositus* workers became more specialized. For *B. bifarius* and *B. flavifrons* workers, greater body size variation was correlated with more generalized foraging, as was higher kurtosis in *B. rufocinctus* and *B. bifarius*.

Mean body size and size variance were positively associated with changes in phenology at the global level across caste (Figure 2.2, Tables S2.8 and S2.10). Earlier emergence and shorter activity periods were associated with smaller bees and less variable body size. For queens, there were species-specific correlations between phenology and the skewness of body size distributions (Tables S2.9 and S2.11). In *B. appositus*, *B. insularis*, and *B. flavifrons*, earlier emergence was associated with negative skewness, suggesting more small-bodied individuals. In these same species, a longer phenological window was also associated with negative skewness.

## Discussion

As the biotic and abiotic environment changes, the mean and spread of trait values admitted by environmental filters may shift, as well as the relative symmetry of those trait distributions and the extent of extreme values (Acevedo-Trejos et al. 2015; Le Bagousse-Pinguet et al. 2017; Hulme & Bernard-Verdier 2018). By considering the four distributional moments – mean, variance, skew, and kurtosis – we can better identify which trait values are gained or lost with abiotic and biotic variation. In our examination of intraspecific trait variation within an assemblage of wild bumble bee species, we find evidence of shifts in body size across all distributional moments, but these responses vary across species and bumble bee social caste. We not only corroborate past evidence of shifts in mean bumble bee body size with variation in climate and floral food resources (Sutcliffe & Plowright 1988; Schmid-Hempel & Schmid-Hempel 1998; Gérard et al. 2020; Zaragoza-Trello et al. 2021; Fitzgerald, Ogilvie & CaraDonna 2022), but also show strong effects of climate on higher moments consistent with trait filtering hypotheses (Box 2.1). When considering the consequences of trait variation, the most conspicuous patterns were that increases in the degree of size variation was strongly associated with dietary generalization, and that changes in phenological activity were correlated with skewed body size distributions in queens. Together, these patterns suggest underlying filtering processes altering trait compositions of these populations, and variation across social castes suggest different demographic forces guiding these trait shifts. Moreover, without considering higher moments of the trait distributions, these patterns would have been obscured.

We find evidence of multiple trait filtering scenarios in response to climate variation (Box 2.1). In queens, we find that early snowmelt conditions decreased mean body size while negatively skewing the size distribution and increasing kurtosis (Figure 2.3). In other words, earlier snowmelt, and therefore shorter winters, leads to a higher frequency of small-bodied queens with an increase in extremely small individuals. In this scenario, these smaller individual queens may not have survived diapause in a longer winter due to reduced energy stores, but under earlier snowmelt are able to successfully emerge (Holm

1972; Schultz & Conover 1999; Vesterlund et al. 2014). For workers, hotter and drier mid-summer conditions were related to increased mean body size, along with decreased variance and kurtosis (Figure 2.4). This pattern suggests the body size distribution of workers becomes both narrower and more evenly distributed, i.e., a more homogenized trait community (Le Bagousse-Pinguet et al. 2017; Gross et al. 2021). Thus, when conditions are hot and dry, the body size distribution of workers shifts and concentrates around larger individuals. Finally, under hotter and drier late-summer conditions, males increased in mean size and decreased in variance without strong changes in higher moments. While it is possible that summer conditions during our study period were sufficiently mild as to not induce developmental or physiological stress (Oyen & Dillon 2018; Kenna, Pawar & Gill 2021), these findings suggest such that larger males are more advantageous, perhaps due to selective pressures related to reproduction (Amin, Bussière & Goulson 2012; Zhao et al. 2021). As the abundance of workers and males for the species we examined mostly do not seem to be strongly correlated with temperature:precipitation ratios in our study system (Ogilvie & CaraDonna 2022), these patterns suggest that hot and dry climate conditions appear to be favourable for larger individuals but the filtering mechanism driving these shifts varies across castes.

Floral resource availability shifted mean size with caste-specific effects on higher moments. Among queens, greater floral abundance was weakly associated with larger individuals at the global level, with no effects on higher moments. Conditional effects varied across species, with *Bombus appositus* showing strong shifts in all four moments (Figure 2.3). For *B. appositus*, the largest species, greater floral resource availability corresponded with increased body size, increased variance, positive skewness, and reduced kurtosis. In other words, higher resource abundance during the developmental period appears to shift the body size distribution towards large queens by increasing the frequency of larger individuals with a loss of and concentration in the frequency of smaller individuals. For workers and males, higher floral abundance was associated with declining mean body size and increased variance without strong global effects on skewness or kurtosis (Figure 2.2). In our system, floral abundance does not consistently

predict the abundance of overwintered queens in spring, but is positively correlated with male and worker abundance (Ogilvie & CaraDonna 2022). Taken together, these observations are consistent with resource allocation strategies such that with greater floral food resources, bumble bee colonies appear to prioritize producing larger “high quality” queens that may be more likely to survive winter diapause and establish colonies (Beekman, Van Stratum & Lingeman 1998; Fitzgerald, Ogilvie & CaraDonna 2022), and that producing a greater frequency of smaller workers and males may be more advantageous for foraging and reproduction (Smith & Fretwell 1974; Stearns 1989).

Consistent with the niche variation hypothesis, we find that mean body size and size variation – but not the higher moments – strongly predicted the degree of foraging specialization at the global level across all castes (Figure 2.4). A greater degree of size variation may facilitate more generalized foraging within a population because a diverse set of traits may allow individuals to use novel or a broader range of resources (Van Valen 1965; Bolnick et al. 2007; Costa-Pereira et al. 2018). In workers, species-specific effects suggest that short-tongued species (*B. rufocinctus*, and more weakly *B. bifarius*) had more generalized foraging with increasing body size whereas longer-tongued species (*B. appositus*, and more weakly *B. flavifrons*) became less generalized. This suggests functional group-specific trait relationships, as the length of the proboscis mediates the depth of the floral corolla an individual is able to extract nectar from and thereby constrains foraging (Inouye 1980; Ranta 1984). As longer-tongued species tend to be larger interspecifically, larger worker body size may further constrain the floral morphologies available to them, while for the smaller, shorter-tongued species, larger worker body size expands the possible foraging resources (Wood et al. 2021). Within a population, individuals of different size classes may forage on specific floral morphologies (Heinrich 1976); changes in the distribution of those sizes classes may alter the identity of the visited plant species without changes in the total richness of diet breadth (Stang et al. 2009; CaraDonna et al. 2017). Thus, there may have been size-related changes in resource use that we could not capture from a summary measure of diet breadth.

Variation in phenology was caste-dependent and largely correlated with changes in mean size and in the skewness of body size distributions, as individuals at the trait tails shift in frequency (Figure 2.4). Our two measures of phenology showed inverse patterns, such that changes in activity period are likely a consequence of earlier emergence and reflect changes in the filtering processes that admit individuals at that tail of the phenological distribution. For example, in *B. flavifrons* queens (the smallest-bodied species) a longer activity period and earlier emergence were correlated with negative skewness. This suggests that more small queens are present, which may have otherwise been filtered out, perhaps by later snowmelt timing or other environmental limits to emergences (*see above*). In contrast, workers showed strong conditional shifts in mean size without strong evidence of changes in other dimensions. This may indicate that when colonies are established earlier in the season, leading to earlier worker emergence, these workers are smaller. In these early season scenarios, it is possible resources are limited for foundress queens, which then go on to produce these smaller workers. The strong conditional correlations between mean size in workers, but less consistent correlation in queens and lack of correlation in males, suggests a demographic link to the role of trait variation. The reproductive role of queens and males may confer a degree of selective stability to their phenology, making them less sensitive to changes in mean size as compared to workers, whose role is more closely tied to colony growth and foraging. Other morphological traits that we did not examine, including body shape, wing length, and tongue length, can also influence bumble bees' resource use and activity in ways that may more strongly explain intraspecific variation in their ecology (Goulson 2003; Heinrich 2004; Le Provost et al. 2021).

The four-moment approach we take here with wild bumble bees provides a more mechanistic understanding of how intraspecific variation is driven by trait filtering processes and how this variation correlates to ecological function (Moran, Hartig & Bell 2016; Green et al. 2022). This framework reveals if and how trait values are lost at the distributional tails, and consequently the broader processes shaping what individuals are present within a population. Looking across multiple species of eusocial bumble bees, we find demographic and functional-group specific patterns of trait variation that may not have been

captured if we had simply considered mean and variance. Our findings provide evidence of strong links between bumble bee body size variation and the abiotic and biotic environment across all four moments, and that variation in size has consequences for both foraging and phenology. Ultimately, considering multiple dimensions of the shape, size, and scale of a trait distribution helps advance our understanding of intraspecific variation and the filtering processes maintaining and shaping populations.

### CHAPTER 3

How does morphological integration and trait scaling influence foraging  
specialization in bumble bees?

## **Abstract**

As organisms scale in size, they also change in shape. With changes in shape often come changes in function. Individual morphological variation can profoundly affect ecological relationships, including diet, reproduction, and movement. While these patterns are well-documented in phenotypically diverse taxa, their role among closely related, morphologically similar species is less resolved. In these groups, ecological differentiation may emerge through subtle variations in trait scaling and integration, mediated by direct functional traits and cognitive correlates, like brain size. Here, we investigate patterns of covariance in foraging-relevant traits and their relationships to diet specialization in wild bumble bees. Compared to other eusocial insects, bumble bees are remarkably similar in morphology, yet commonly overlap in space, time, and foraging. We primarily found hypoallometric scaling relationships: larger bees had proportionally smaller heads and pollen load capacity. Larger head to body ratios, i.e., larger brain volumes, were positively associated with more generalized diets in queens and workers, and higher trait integration was positively correlated with diet breadth in workers. Our findings suggest that small differences in trait covariation can have large consequences for species function, with adaptive patterns of variation across species and social caste that may promote the co-occurrence of morphologically similar groups.

## **Introduction**

Variation in organismal form underlies considerable variation in ecological function (Wainwright and Reilly 1994; Calder 1996), yet many sympatric species occupy similar ecomorphological spaces (Kolbe et al. 2011; Guillemain et al. 2002). How then do multiple species, which are both morphologically and ecologically similar, co-occur? Trait variation within and among individuals can strongly shape the way organisms interact with each other and their environment (Abbott, Abbott, and Grant 1977; Weiher, Clarke, and Keddy 1998; Turcotte and Levine 2016), and can scale to influence higher-level ecological processes including dispersal, reproduction, and foraging (Retana and Cerdá 1994; Tomkins, Kotiaho, and

LeBas 2005; Okada, Nomura, and Miyatake 2007; Solida et al. 2007). Beyond differences in gross morphology, however, subtle trait variation may manifest through two complementary mechanisms: trait scaling relationships and patterns of trait integration. Whereas allometric scaling describes how individual traits change with body size (Enquist et al. 2003; Schmidt-Nielsen 1975), trait integration (i.e., the degree of intercorrelation among multiple traits) characterizes how traits function as coordinated systems rather than isolated components (Olson and Miller 1958). Among closely related taxa with relatively similar morphologies, ecological differentiation may then emerge from these two processes (Melville and Swain 2000; Šimková et al. 2002; Daskin et al. 2023). Thus, this seeming paradox of morphologically and ecologically overlapping species may suggest that subtle differences in trait variation can influence resource and niche partitioning.

Body size is an important contributor to both morphological and ecological variation as some traits scale at a steeper rate than others – that is, large individuals are not necessarily proportionally sized-up versions of smaller individuals (Figure 3.1) (Huxley 1932; Schmidt-Nielsen and Knut 1984; West, Brown, and Enquist 2000). Metabolic theory predicts a three quarter power law such that as body size increases, other traits increase at a slower rate relative to their volume and surface area, including, for example, circulatory systems, brain size, and limbs (Kleiber 1947; Agutter and Tuszynski 2011). Yet, in contrast to the moderate scaling predicted by theory, we frequently observe exaggerated scaling in nature, which is often strongly linked to ecological function (Emlen and Nijhout 2000). This allometric scaling is especially evident in extreme sexually-selected traits, such as the major claw of fiddler crabs or the antlers of male deer, where larger individuals have increasingly larger ornamentation (hyperallometric scaling; Huxley 1924; Rodríguez and Eberhard 2019). Functional scaling is also relevant among less conspicuous traits, such as the flagellum of ant antennae, which become relatively shorter as body size increases (hypoallometric scaling; Tschinkel, Mikheyev, and Storz 2003), such that smaller individual workers have a greater density of olfactory sensilla (Keil 1999). While metabolic theory predicts relatively moderate scaling relationships, the prevalence of exaggerated scaling (both hyper- and hypoallometric)

suggests that variation in individual body size within and among species can have strong and non-linear effects on ecological function (Marshall et al. 2021; Nørgaard et al. 2022).

Among sets of traits across an individual, variation in the magnitude and direction of allometric scaling can affect the degree of covariance across morphological structures (e.g., limb proportions) or the whole organism (Figure 3.1). Changes in patterns of trait covariation often reflect changes in function (Ricklefs, Cochran, and Pianka 1981; Kolbe et al. 2011). For instance, in seed-harvesting *Pheidole* “big-headed” ants, there are two discrete dimorphic worker castes with unique trait covariance patterns (Holley et al. 2016; Friedman et al. 2020). Large “major” workers have exaggerated and specialized jaws for colony defense and processing seeds for food as compared to “minor” workers, who are more morphologically moderate and behaviorally generalized. Similar patterns of increased functional performance with increased morphological integration have been observed in many systems, such as the humerus of moles derived for digging (Sansalone et al. 2022), and the mandible of aquatic-foraging snakes (Rhoda et al. 2021). Sets of functionally relevant traits covarying in a coordinate manner may then suggest specialized ecological performance (Randau, Sanfelice, and Goswami 2019; Yuan, Wake, and Wang 2019).

These patterns of trait covariation exist along a continuum. While trait differences are obvious in extreme organismal forms, more subtle morphological variation may still have functional consequences. For example, complex foraging may impose cognitive demands that lead to hyperallometry between body and head size (Lefebvre et al. 1997; Axelrod, Laberge, and Robinson 2018), such that individuals of different sizes have allometric cognitive capacities, which can contribute to dietary niche partitioning across species (Mace, Harvey, and Clutton-Brock 1981; Kotrschal et al. 2013; Feinerman and Traniello 2016). If relative brain size also strongly covaries with other foraging-relevant traits, that is, exhibits a high magnitude of integration, this may suggest an adaptive tendency of the whole organism to covary to facilitate foraging (Ferry-Graham, Bolnick, and Wainwright 2002; Klingenberg 2008). A high degree of integration indicates that possible morphological variation is relatively restricted (Figure 3.1) (Machado et

al. 2019). In this scenario, a particular form may be favored such that species with high integration may exhibit more specialized foraging, while those with lower integration may have more flexible foraging (Berg 1960; Mehta 2009; Monteiro and Nogueira 2010; Michaud, Veron, and Fabre 2020). Alternatively, greater integration may be associated with more generalized foraging if there is a preferred form for exploiting a greater variety of resources, that is, a morphological jack-of-all-trades (Olson and Miller 1958).

In some species, there can be dramatic ecomorphological differences between sexes or life stages, or in the case of eusocial insects, among castes. Sometimes, however, clear functional differences are not matched by clear morphological differences, such as in the case of bumble bees (*Bombus* spp.). Arguably a “morphologically monotonous” group (Michener 1990), bumble bees are globally widespread and largely generalist pollinators, and despite their biogeographic and ecological breadth, sympatric species are largely distinguished by pile color patterns and body size. Even among outlier species, such as *B. dahlbomii*, the world’s largest bumble bee in Patagonia, *B. sonorous*, a desert-dwelling species, or *B. polaris*, found exclusively above the arctic circle, bumble bees are remarkably similar in form across species. As a group, bumble bees are primitively eusocial, where reproductive females (queens) are distinguished from non-reproductive females (workers) primarily by size (Plowright and Jay 1968). While the body size of workers can vary enormously within a colony, there otherwise are not obvious phenotypic polymorphisms or subcastes (Goulson 2010).

Yet, bumble bee workers of different sizes perform distinct functional roles in the colony (Plowright and Lavery 1984). Larger bodied workers are more likely to forage than smaller bodied “nurse” bees, which tend to stay in the nest and care for brood (Robinson 1992; Holland et al. 2021). These larger workers may have distinct trait covariance patterns that enhance their foraging abilities as compared to their smaller sisters, and their brothers, which leave the natal nest to disperse and find mates (Friedman, Remeš, and Economo 2019). In a simple example, hyperallometric scaling between body size and corbicula length (i.e., the pollen basket) would indicate that larger-bodied workers have

disproportionately larger corbiculae, which may enhance their foraging efficiency and resource collection capacity. If this scaling is also highly integrated with head width scaling, then larger workers may also have disproportionately larger brain volumes. Larger bodied workers would then have both greater cognitive abilities and pollen load capacity, suggesting adaptive covariance to promote foraging. We may then predict that any such trait relationship patterns promote functional differences in foraging abilities between and within social caste.

To examine how individual variation may influence ecological differentiation among morphologically similar groups, we investigate trait covariation patterns and their relation to caste and foraging in an assemblage of wild bumble bees in the Colorado Rocky Mountains, USA. We consider three morphological traits, including a whole-body size estimate and two traits proposed to influence bumble bee foraging (Figure 3.1). We then ask the following: (1) How do traits scale and integrate across different body sizes? (2) How do trait covariance patterns relate to dietary niche breadth? We additionally consider how these processes play out across social castes. By examining the relationships between traits and foraging, our work helps to clarify the relative importance of form to function and offers insights into the broader processes that shape the maintenance of morphologically similar species.

## Methods

### Study system

We monitored bumble bee species across three growing seasons (2020-2022) in subalpine meadows near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA (2,900 m a.s.l.). We considered seven *Bombus* species, spanning a range of body sizes and relative foraging specializations, and overlapping in their phenological activity: *B. appositus*, *B. bifarius*, *B. californicus*, *B. flavifrons*, *B. insularis*, *B. nevadensis*, and *B. rufocinctus*. Bumble bees are the numerically dominant members of the pollinator community in this area, where non-native bees, including *Apis mellifera*, the European honey bee, are absent. Typical of other high-elevation and high-latitude systems, the area is highly seasonal with

a short growing season beginning with spring snowmelt (April-June) and ending in the early fall (September-October) (CaraDonna, Iler, and Inouye 2014).

### Morphological sampling

From early spring when queens emerge to the beginning of fall after male emergence, we surveyed six previously established sites twice a week (Ogilvie and CaraDonna 2022). During each survey period, we non-destructively hand-netted active bees for a minimum of one hour of sampling effort, alternating visiting each site in the morning (9:00–12:00 h) and afternoon (13:00–17:00 h) to represent a range of foraging conditions. From each individual that we hand-netted, we collected three morphological measurements (Figure 3.1): (1) intertegular distance (ITD), the space between the wing bases on the abdomen and a common and robust measure of bee body size (Cane 1987; Hagen and Dupont 2013); (2) head width, measured across the widest part of the eyes and representing brain size (Mares, Ash, and Gronenberg 2005; Riveros and Gronenberg 2010); and (3) corbícula length, the outer side of the hind tibia, representing the volume of the pollen basket (Eggenberger et al. 2019).

It is generally hypothesized that brain size is positively correlated with behavioral complexity, which may then allow for greater performance under cognitively demanding tasks (Kondoh 2010; Edmunds, Laberge, and McCann 2016; Herczeg et al. 2019). In bumble bees, greater brain size may allow for more complex and flexible foraging, including more generalized floral resource use, handling of complex floral morphologies, and frequent resource switching (Riveros and Gronenberg 2010; Feinerman and Traniello 2016). If the ratio of head width to body size is low, this may indicate a relatively small brain size, and consequently more simplified foraging (*but see* Sayol et al. 2020).

Corbícula length partially determines the volume of pollen a queen or worker is capable of collecting and returning to the colony during a foraging trip (Eggenberger et al. 2019). The pollen load capacity of an individual generally increases with body size (Free 1955a), however the relative ratio of the corbícula length to overall size may not be directly proportional (Ramalho, Imperatriz-Fonseca, and

Giannini 1998). For instance, a hypoallometric scaling relationship between pollen load capacity and body size may allow smaller overall workers to contribute proportionally greater volumes of pollen to the colony (Goulson et al. 2002; *but see* Kerr, Crone, and Williams 2019). Note that male bumble bees and cuckoo species from the *Psithyrus* subgenus, including *B. insularis* in our study, do not have corbicula.

### Analytical framework

We employed two complementary sampling unit approaches to examine trait covariance relationships. First, to capture fine-scale patterns of trait variation, we defined sampling units as each unique species-caste measurement combination at each survey site ( $N = 6$ ) in each year (2020-2022,  $N = 3$ ), requiring at least 5 individuals to be measured for a total of 145 units across species. Second, to analyze broader patterns of trait covariance and diet breadth (see below), we defined sampling units for each species-caste combination ( $N = 17$ ). We computed scaling relationships and morphological integration at each of these levels as described in the following sections.

### Scaling relationships

To characterize the scaling relationships between body size and head width and corbicula length, we used a series of standardized major axis estimations using the R package *smatr* (Warton et al. 2012). This analytical approach is a symmetric regression from the geometric mean and accounts for variation in both variables, as compared to an ordinary least squares approach using linear regressions, where one variable is predicted from another. We fit slopes for each sampling unit independently. These slopes represent  $a$ , the scaling coefficient for a given trait relationship (Figure 3.1). If  $a = 1$ , this indicates a directly proportional isometric relationship. If  $a > 1$ , this indicates hyperallometric scaling, meaning, for example, that head width increases at a faster rate than body size. Conversely, if  $a < 1$ , this indicates hypoallometric scaling, such that head width increases at a shallower rate than body size.

### Morphological integration

We defined morphological integration – the overall level of inter-correlation among traits – as the variance in eigenvalues from a correlation matrix for each trait pairing across each sampling unit (species-caste-site-year and species-caste, see above). Higher relative eigenvalue variance corresponds to higher levels of integration, as a large proportion of the total variance is captured by a few dominant eigenvectors. Conversely, lower values suggest a more even distribution of variance. We calculated eigenvalue variance ( $Var(\lambda)$ ) as the average square deviation of eigenvalues from the mean eigenvalue (which is always equal to one in a correlation matrix), normalized by dividing by the number of traits ( $N$ ) in the matrix (Pavlicev, Cheverud, and Wagner 2009):

$$Var(\lambda) = \frac{\sum_{i=1}^N (\lambda_i - 1)^2}{N}$$

Because not all three traits are represented in all castes (e.g., males do not have corbicula), we then calculated relative eigenvalue variance ( $Var_{rel}(\lambda)$ ) as the observed eigenvalue variance over the maximum eigenvalue variance for a set of traits:

$$Var_{rel}(\lambda) = \frac{Var(\lambda)}{N - 1}$$

This relative value is therefore independent of the number of traits, spans 0 to 1, and can be used to compare overall integration levels across species and castes (Figure 3.1).

### Quantifying resource use

We estimated diet breadth for each species and caste combination using highly resolved, long-term visitation data in our sites (Ogilvie and CaraDonna 2022). These data were collected weekly across the growing season, for one hour of sampling effort at each site, and represent what plant species each *Bombus* species was observed visiting. From these data, we constructed a binary visitation incidence matrix for each species and caste combination at each site ( $N = 6$ ) over our three study years (2020-2022,

$N = 3$ ). These matrices represent whether a plant species was observed being visited in each site-year combination for each species-caste group.

To describe the diversity of each species' diet, we used the iNEXT package (Hsieh, Ma, and Chao 2016), which computes rarefaction and extrapolation sampling curves, to estimate Hill-Shannon diversity of each bee species' foraging interactions. Hill diversity is a generalized diversity metric that is calculated as:

$${}^qD = \left( \sum_{i=1}^S p_i^q \right)^{1/(1-q)}$$

where  $D$  represents diversity (in this case, diet breadth diversity),  $S$  is the number of species (here, plant species interacted with),  $p_i$  is the proportion of all interactions belonging to plant species  $i$ , and  $q$  is a parameter weighting the contribution of each species according to their rarity. Here, we set  $q$  to 1, which is equivalent to the familiar Shannon diversity:

$${}^1D = \lim_{q \rightarrow 1} {}^qD = \exp - \left( \sum_{i=1}^S p_i \log p_i \right)$$

in which species are weighted according to their proportional contribution to the assemblage (Chao et al. 2014).

We then standardized diet breadth estimates at 95% sample coverage, where coverage ( $C$ ) measures sample completeness as:

$$C = 1 - \frac{f_1}{n} \left[ \frac{(n-1)f_1}{(n-1)f_1 + 2f_2} \right]$$

with  $f_1$  and  $f_2$  representing the number of singleton and doubleton species occurrences, respectively, and  $n$  being the total number observed visits (Roswell, Dushoff, and Winfree 2021). This approach minimizes the influence of rarely visited species while accounting for undetected species through extrapolation (Chao and Jost 2012). Thus, our diet breadth measure provides a robust estimate of the effective number of plant species visited by each species-caste group.

### Statistical analyses

We conducted all analyses in R Statistical Computing Software (v4.2.2; R Core Team 2022) using a series of Bayesian models using the package *brms* (Bürkner 2017). We employed four Markov chains with 4000 cycles, each with a 2000-iteration warmup phase, adjusted smoother sampling behavior and Markov chain convergence by setting the `adapt_delta` parameter to 0.99, and evaluated model fit using the Gelman-Rubin statistic  $\hat{R}$  (“R-hat”).

We first modeled how the direction and magnitude of the scaling relationships of head width and corbícula length varied with overall body size. For each model, we included the mean body size within each sampling unit (species-caste-site-year) as a fixed effect interacting with caste to estimate separate slopes for queens, workers, and males. In these scaling models, we specified normal priors for the intercept ( $\mu = 1$ ,  $\sigma = 0.5$ ), centered on 1 to represent isometric scaling, and weakly informative normal priors ( $\mu = 0$ ,  $\sigma = 1$ ) for body size and caste effects, as well as their interactions. Using a similar modeling framework, we also asked how the degree of morphological integration (measured as the covariance between traits) varied by mean body size and caste. As integration is bounded between 0 and 1, we defined a beta prior ( $\alpha = 1.5$ ,  $\beta = 1.5$ ) for the intercept, with similarly weakly informative normal priors ( $\mu = 0$ ,  $\sigma = 1$ ) for size and caste effects. These priors reflect expected biomechanical and developmental constraints on trait scaling and covariance, for example, we do not expect extremely exaggerated scaling.

We then modeled diet breadth as a function of three trait relationships: mean body size, relative head size, and morphological integration. Here, our sampling unit is each unique species-caste combination. We constructed Bayesian generalized linear models for each trait relationship with the respective predictor included as a fixed effect interacting with caste. We used a Gamma distribution and log link function to account for the bounded, positive, and right-skewed diet breadth values. We assessed evidence for effects based on whether credible intervals (CI) overlapped zero and interpreted the strength of effects using the width and location of these intervals. We consider effects to be strong when  $\geq 90\%$

credible intervals exclude zero, meaning that at least 90% of the predictions are for non-zero patterns. We consider moderate evidence to be when 80% intervals exclude zero, and weak or uncertain when intervals overlap zero more substantially.

## Results

We measured the morphology of 2,423 individual bumble bees across seven species: *B. appositus*, *B. bifarius*, *B. californicus*, *B. flavifrons*, *B. insularis*, *B. nevadensis*, and *B. rufocinctus*. Mean body size varied substantially among species and caste, where the largest bees, *B. nevadensis* queens (intertegular distance;  $\mu = 7.14 \pm 0.17$  mm), were, on average, nearly three times larger than the smallest bees, *B. rufocinctus* workers ( $\mu = 2.40 \pm 0.03$  mm) (Table S3.1).

### *Trait covariance patterns*

Across individuals of different sizes, bumble bees vary in their trait relationships, with caste-specific patterns (Figure 3.3). As mean body size increased, workers head widths scaled moderately more hypoallometrically ( $\beta_{\text{head width}} = -0.17$ , 80% CI: [-0.34, -0.01]), corbicula lengths trended towards weaker allometry ( $\beta_{\text{corbicula length}} = -0.12$ , 60% CI: [-0.24, -0.01]), and trait integration strongly declined ( $\beta_{\text{integration}} = -0.11$ , 95% CI: [-0.22, -0.01]). In other words, larger individual workers tended to have comparatively smaller heads and corbicula, with much lower trait covariation (Tables S3.2, S3.3, and S3.4).

In queens, as mean body size increased, head widths trended towards weaker allometry ( $\beta_{\text{head width}} = -0.05$ , 60% CI: [-0.10, -0.001]), whereas corbicula length strongly scaled hypoallometrically ( $\beta_{\text{corbicula length}} = -0.22$ , 99% CI: [-0.40, -0.06]), and trait integration very weakly declined ( $\beta_{\text{integration}} = -0.02$ , 60% CI: [-0.04, -0.004]) (Tables S3.2, S3.3, and S3.4). For males, head width scaling was not correlated with mean body size ( $\beta_{\text{head width}} = 0.13$ , 50% CI: [-0.09, 0.35]) and there was strong evidence that trait integration was higher in larger individuals ( $\beta_{\text{integration}} = 0.28$ , 95% CI: [0.02, 0.54]).

### *Correlations between trait covariance and diet breadth*

Morphological variation had strong effects on bumble bee diet breadth, but the consequences of morphology varied by trait relationship and caste (Figure 3.4). There was a wide range of diet breadth among bumble bee species and castes, ranging from highly specialized *B. nevadensis* workers ( $^1D = 6.02$ ) to highly generalized *B. bifarius* workers ( $^1D = 38.03$ ). As mean body size increased, diet breadth strongly decreased in queens and workers ( $\beta_{\text{queens}} = -0.40$ , 99% CI: [-0.63, -0.14],  $\beta_{\text{workers}} = -0.87$ , 99% CI: [-1.26, -0.48]) (Table S3.5 and Figure 3.4). As the scaling relationship between head width and body size increased (i.e., as relative brain size increased), queen diet breadth strongly increased ( $\beta_{\text{queens}} = 4.24$ , 95% CI: [0.53, 0.841]) and worker diet breadth moderately increased ( $\beta_{\text{workers}} = 2.35$ , 70% CI: [0.25, 4.56]) (Table S6). As the degree of morphological integration increased, worker diet breadth strongly increased ( $\beta_{\text{workers}} = 4.16$ , 95% CI: [0.31, 7.34]), whereas queen diet breadth was not correlated ( $\beta_{\text{queens}} = -1.16$ , 50% CI: [-2.45, 0.192]) (Table S7). In males, diet breadth was not correlated with any trait relationship we considered ( $\beta_{\text{mean size}} = -0.21$ , 50% CI: [-0.47, 0.05],  $\beta_{\text{head width scaling}} = -0.08$ , 50% CI: [-0.78, 0.71],  $\beta_{\text{morphological integration}} = 0.10$ , 50% CI: [-1.73, 1.86]) (Figure 3.4).

## **Discussion**

As individuals scale in size and vary in shape, nearly every measurable aspect of an organism also changes (Bergmann 1848; Thomson 1917; Kleiber 1947; Krebs 1950; Stanley 1973; Wilson 1975; Woodward et al. 2005). Understanding how variation in form links to function can provide insights into the forces driving niche differentiation, particularly among superficially similar groups (Losos 1990; Wellborn and Cothran 2004; Smith et al. 2011; Hart, Schreiber, and Levine 2016; Žagar et al. 2017). Here, we investigated trait covariance and their relationships to foraging in an assemblage of wild bumble bees that overlap phenologically, ecologically, and morphologically – a scenario in which we might

expect strong character displacement but instead observe broadly similar morphologies. Yet, despite this seeming contradiction between overlapping form and function, our analyses suggest that relatively small variations in trait covariance can translate to functional differences and may indicate adaptive patterns of morphological variation.

We find evidence of functionally relevant allometric trait scaling across social castes. These patterns suggest that bumble bees of different sizes are not proportionally scaled ecological equivalents. Queens and workers mostly exhibited hypoallometric scaling relationships between body size, head width, and corbicular length, such that larger individuals had proportionally smaller heads and corbicula than smaller individuals (Figure 3.4). The strength of these hypoallometric relationships increased with increasing body size. In queens, there was strong evidence for increasingly hypoallometric corbicular scaling, meaning that the very largest queens exhibited the smallest pollen baskets relative to their body size. In workers, relative head width moderately decreased with increasing body size. Thus, relative brain size, represented by the ratio between head width and overall body size, is smallest among the very largest individuals. Hypoallometric brain scaling is common across most animals, potentially due to the energetic constraints related to the metabolic cost of the brain (Burger et al. 2019). Generally, larger brains allow increased information processing, which is partially a consequence of larger neurons (Chittka and Niven 2009). In eusocial insects, who have complex behavioral repertoires for their relatively small brains, there may be diminishing returns for increasingly large brain sizes (Mares, Ash, and Gronenberg 2005; Riveros and Gronenberg 2010).

In our study, the relationship between relative brain size and diet breadth was caste-specific (Figure 3.4). For queens, and more weakly for workers, as relative brain size increased, diet breadth also increased, i.e., proportionally larger brained female bees had broader diets. Larger relative brain size is often associated with increased behavioral complexity (Marino 2005; Schuck-Paim, Alonso, and Ottoni 2008), indicating that larger brain volumes in queen and worker bumble bees may translate to marginally more flexible use of floral resources (Collado et al. 2021; *but see* Sayol et al. 2020). These caste-specific

trends may reflect differences in cognitive ability (Wolf and Chittka 2016; Muth et al. 2021). Queens live for a full year, during which time they must handle a wide suite of novel resources, disperse from their natal nests, and identify suitable hibernaculum and nest sites (Goulson 2010). Workers, while shorter lived than queens, also exhibit a broad behavioral repertoire, including foraging, brood care, and complex division of labor within the colony (Free 1955b). Collectively, these behaviors may impose additional cognitive demands on the queens and workers not present in less behaviorally complex males, which leave the natal nest to mate, do not contribute to colony-level labor, and survive for just a few weeks (Muth 2021).

Many other traits likely contribute to the degree of bumble bee foraging specialization and scale allometrically with body size. Examples of these traits include tongue length (Harder 1982; Waddington and Herbst 1987), which mediates the types of flowers a bee can extract nectar from (Inouye 1980; Inoue and Yokoyama 2006), and the size of sensory organs which regulate visual and olfactory acuity (e.g., ommatidia and flagellomers) and may allow larger-bodied individuals to better locate and differentiate floral resources (Spaethe and Chittka 2003; Kapustjanskij et al. 2007; Spaethe et al. 2007; Kelber and Somanathan 2019; Taylor et al. 2019). As these traits are difficult to sample non-destructively in the field, we did not include them in our study. However, longer-tongued species tend to be more specialized foragers (Wood et al. 2021) in part because they also tend to be larger-bodied (Cariveau et al. 2016), and may therefore be able to competitively dominate higher-quality nectar resources (Bowers 1985; Fitzgerald, Ogilvie, and CaraDonna 2022). Thus, larger relative brain size in smaller bees may be an adaptive strategy to facilitate a need to visit a greater variety of resources (i.e., more brain, less brawn).

We additionally considered how the pollen resource acquisition capacity of foraging queens and workers covaried with body size. We found that corbicula length and body size also generally scaled hypoallometrically (Figure 3.4), suggesting that smaller-bodied queens and workers can transport comparatively larger pollen loads back to the nest. Corbicula length is a proxy for maximum potential pollen load and may not directly translate to volume of pollen returned to the colony, which may vary

depending on the length of time an individual has been foraging and the available pollen resources. However, the hypoallometric relationships we observed suggest that smaller individuals have a proportionally higher pollen load capacity. This may suggest a tendency to maximize colony-level fitness benefits by producing smaller, developmentally “cheaper” workers, who may contribute a smaller overall pollen load but a greater relative volume per foraging bout (Fitzgerald, Ogilvie, and CaraDonna 2022; *but see* Kerr, Crone, and Williams 2019).

Next, we asked how this mosaic of traits covaried across the whole organism. The focal traits in our study have distinct developmental pathways and are therefore unlikely to represent structural covariation (Klingenberg 2008). However, they each reflect morphological adaptations that influence the detection and acquisition of floral food resources and may therefore be functionally related. Relatively high trait integration suggests that phenotypic variation is restricted to a few dimensions of morphological space, and conversely, low integration suggests traits may vary somewhat independently of each other (Olson and Miller 1958; Machado et al. 2019). We initially predicted that high morphological integration may then reflect an adaptive strategy, wherein stronger integration suggests restricted morphological variation that facilitates more specialized foraging. We instead find conflicting and caste-specific associations between integration and dietary resource use (Figure 3.4). The strongest pattern is that more morphologically integrated workers had greater diet breadth, i.e., more generalized foraging, whereas there was not an association between integration and foraging breadth in queens and males. Larger, less integrated workers are also more specialized in their foraging patterns (Figures 3.3, 3.4). This is consistent with the hypothesis that generalized “jack-of-all-trades” foragers are more morphologically constrained (Van Valen 1965; Mehta 2009; Michaud, Veron, and Fabre 2020). Variation in the magnitude of trait correlations may reflect distinct foraging adaptations to specific groups of floral resources or floral morphologies, which may not be represented in our relatively high-level measure of diet breadth. Additionally, workers are the primary foragers for the colony and may therefore show stronger patterns of functional links between our focal traits and diet breadth. In contrast, queens and males, who are solitary

foragers, showed no correlation between diet breadth and trait integration, suggesting different demographic pressures on morphology.

Taken together, we find that subtle morphological variations among individuals can have large consequences for dietary resource use, such that if we were to assume isometry or other simple patterns, we may miss important functional relationships. Given recent evidence of shifting bumble bee body size (Fitzgerald, Ogilvie, and CaraDonna 2022; Gérard et al. 2021), understanding individual-level patterns of trait covariance is likely to be important for predicting the consequences of changing trait distributions. The observed shifts in bumble bee body size are complex and driven by a variety of factors, such as land use change (Theodorou et al. 2020; Gérard et al. 2020), and altered temperature regimes (Nooten and Rehan 2020; Oliveira et al. 2016), consistent with broader trends of declining animal body size with climate change (Gardner et al. 2011; Sheridan and Bickford 2011). In addition, these distributional shifts are not necessarily symmetric or even (Fitzgerald, Ogilvie, and CaraDonna 2024). Individuals at the distributional tails may have unique morphological traits, as observed here, such that the loss or addition of these outlier individuals may have disproportionate ecological consequences (Violle et al. 2017; Van Valen 1965).

At broad strokes, bumble bees are remarkably similar in morphology. Outside of obvious differences in size between castes and species, bumble bees do not exhibit extreme trait forms like those seen in many other eusocial insects (e.g., soldier ant subcastes, alate termites). Yet, our results highlight that relatively small variations in morphology can translate to large differences in species foraging and consequently may reflect distinct adaptive patterns of trait variation. Ultimately, phenotypic variation is a key contributor to species function, and trait covariation patterns have the potential to maintain the co-occurrence of morphologically similar groups.

## TABLES AND FIGURES

**Table 1.1.** The number of papers that explicitly consider external environmental drivers or ecological consequences of bumble bee body size variation from a within-species (intraspecific) or between-species (interspecific) perspective, or both. (See Table S1.1)

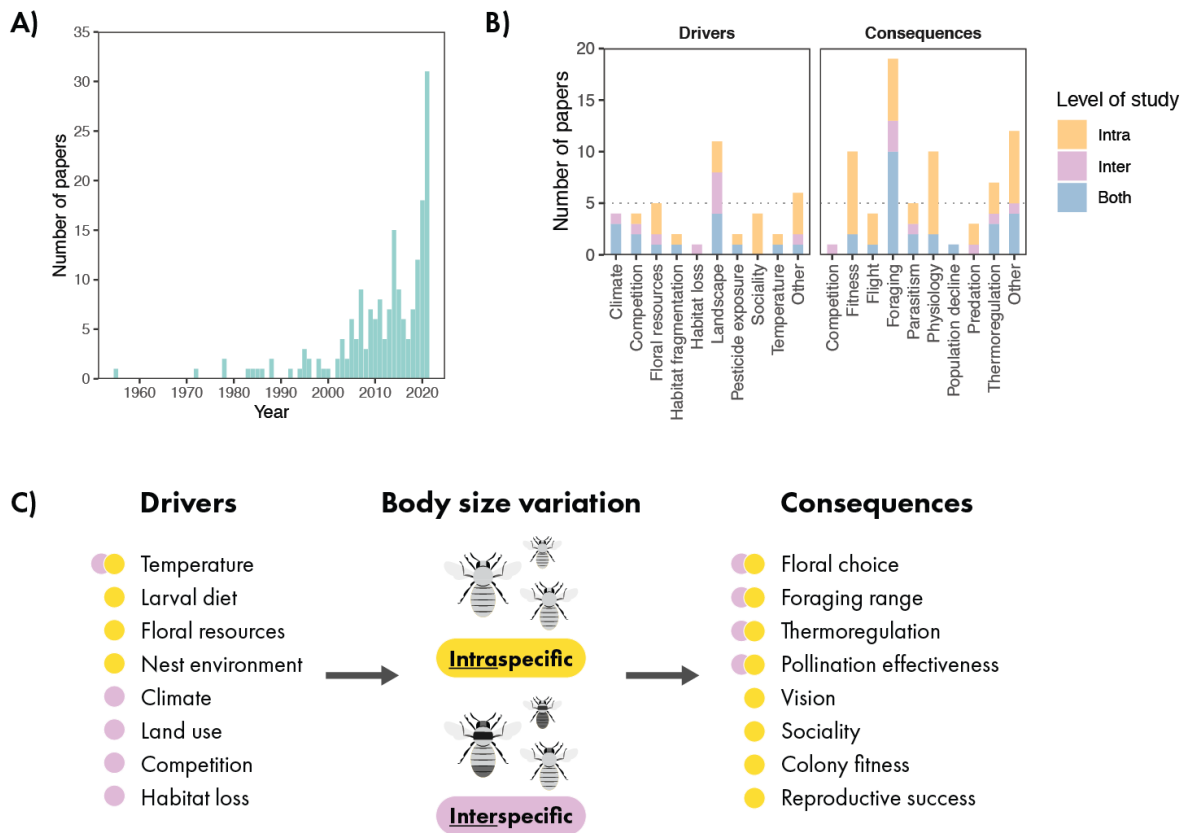
|                                | Number of papers |               |              |
|--------------------------------|------------------|---------------|--------------|
|                                | Interspecific    | Intraspecific | <i>Total</i> |
| <b>Ecological drivers</b>      |                  |               |              |
| Climate                        | 7                | 6             | 7            |
| Competition                    | 4                | 4             | 5            |
| Floral resources               | 2                | 9             | 10           |
| Habitat fragmentation          | 1                | 2             | 2            |
| Habitat loss                   | 1                | 0             | 1            |
| Landscape <sup>a</sup>         | 15               | 13            | 20           |
| Pesticide exposure             | 1                | 2             | 2            |
| Temperature                    | 5                | 8             | 8            |
| Other                          | 1                | 5             | 5            |
| <b>Ecological consequences</b> |                  |               |              |
| Competition                    | 1                | 0             | 1            |
| Fitness                        | 15               | 13            | 15           |
| Flight                         | 1                | 8             | 8            |
| Foraging <sup>b</sup>          | 25               | 31            | 37           |
| Parasitism                     | 6                | 9             | 10           |
| Physiology <sup>c</sup>        | 3                | 16            | 16           |
| Population decline             | 5                | 5             | 5            |
| Predation                      | 1                | 2             | 3            |
| Thermoregulation               | 6                | 12            | 13           |
| Other                          | 5                | 21            | 21           |

<sup>a</sup> Includes agriculture, urbanization, corridors, forest cover, wildfire

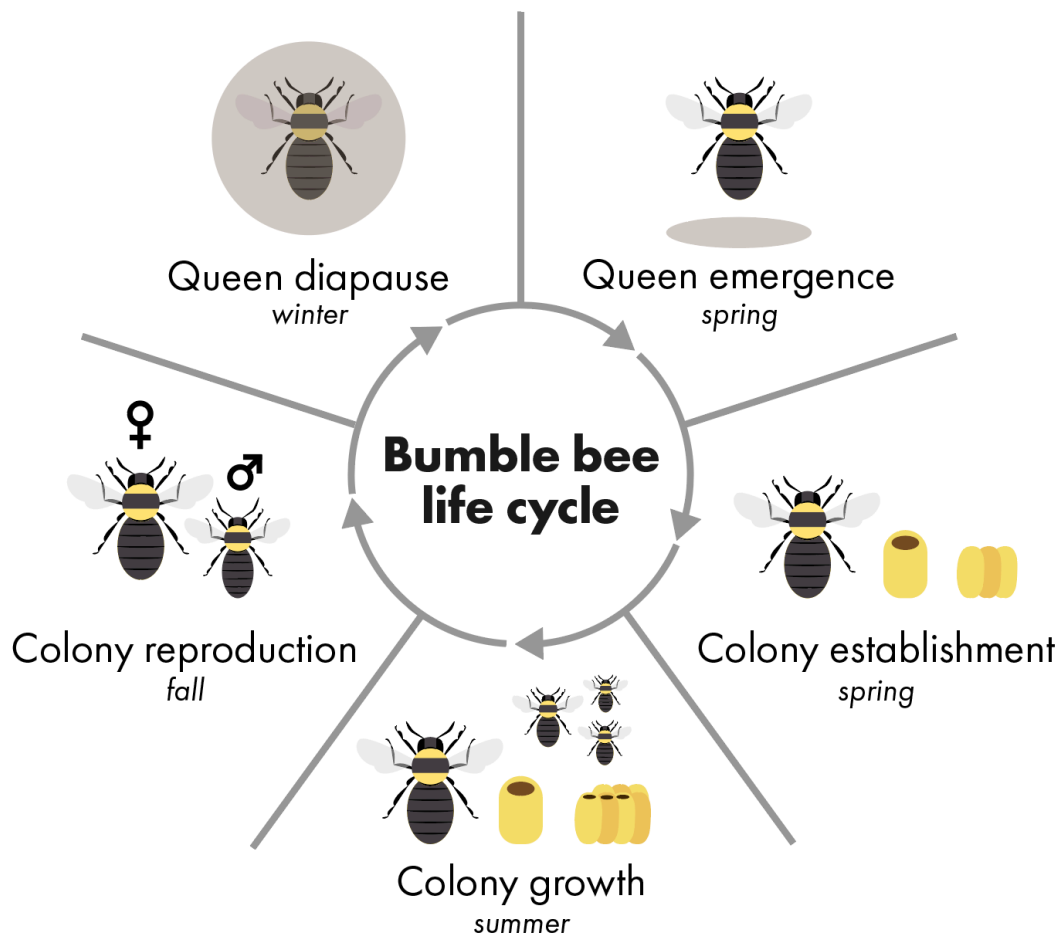
<sup>b</sup> Includes foraging range, foraging rate, pollination effectiveness, floral choice

<sup>c</sup> Includes vision, olfaction, circadian rhythms, immunocompetence

**Figure 1.1.** A) Size variation between a *Bombus flavifrons* queen (left), worker (center), and male (right); B) Size variation between *B. californicus* queen (left) and worker (right); C) Size variation within *B. bifarius* workers. Specimens from the Rocky Mountain Biological Laboratory research collection.

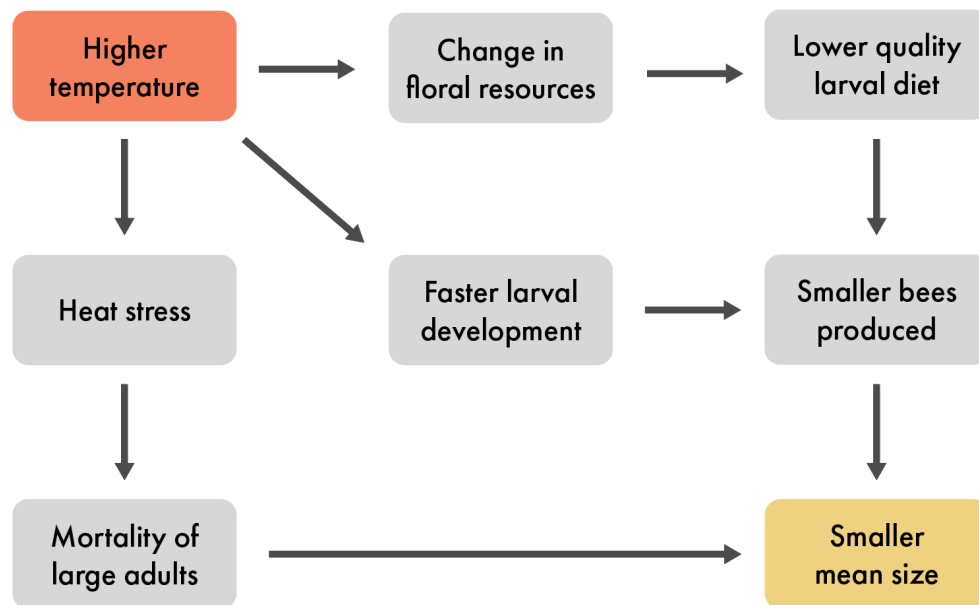


**Figure 1.2.** (A) Number of papers on the drivers or consequences bumble bee body size across time. (B) Number of papers on the drivers and consequences of bumble bee body size divided by category and by the level of organization the paper considers: within species (*intraspecific*), between species (*interspecific*), or both. (C) Specific drivers and consequences of size variation within (*intraspecific*) and between species (*interspecific*).

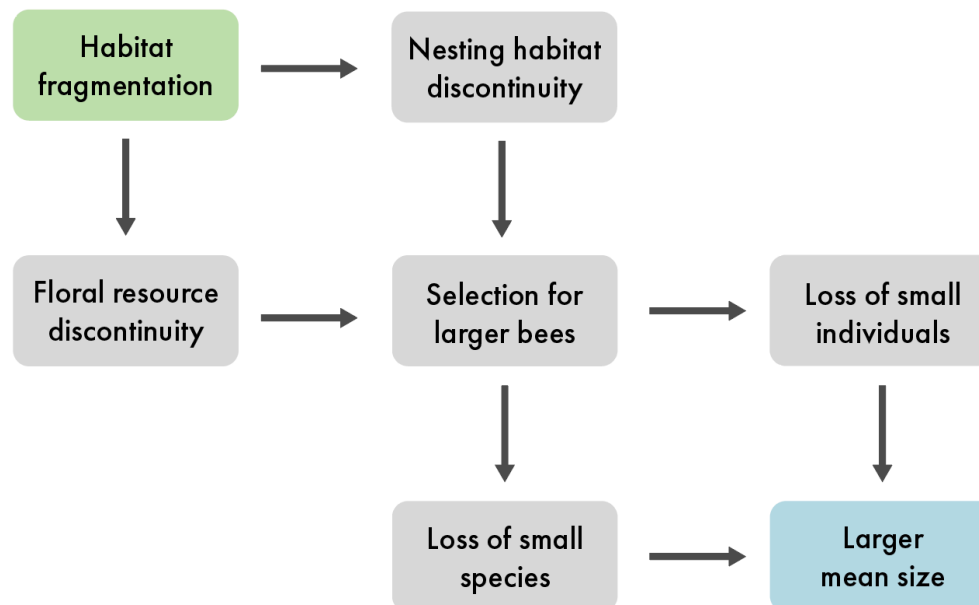


**Figure 1.3.** Annual life cycle of a bumble bee colony. In the spring, bumble bee queens that were born the previous fall emerge from winter diapause and begin to forage. Queens that successfully found a nest will go on to produce a colony of workers. Towards the end of the growing season, the colony will produce sexual new queens and males. New queens will mate and enter diapause.

A)



B)

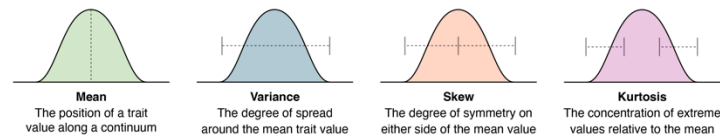


**Figure 1.4.** (A) Hypothetical pathways by which higher temperatures could lead to smaller mean body size in bumble bees. Developmentally, higher temperatures could lead to smaller bees through the temperature-size rule or indirectly through changes in floral resources affecting larval nutrition. For adult bees, size-based differences in thermal tolerance could lead to the mortality of large individuals. These hypotheses are not mutually exclusive, multiple pathways could be acting simultaneously.

(B) Hypothetical pathways by which habitat fragmentation could lead to larger mean body size in bumble bees. Discontinuity of resources selects against small bee species and small individuals that have lower dispersal ability and are unable to traverse large distances or meet their caloric needs from small, isolated patches. The specific effects of habitat fragmentation may be difficult to disentangle from the effects of habitat loss and land use change, which may impose contrasting pressures on size.

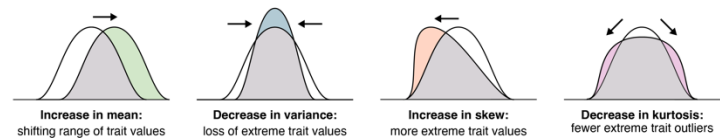
## Trait distribution dimensions

The distribution of a trait within a population can be described by multiple dimensions, called moments, including central tendency, the spread of values, the relative symmetry, and the presence and extent of outlier values.



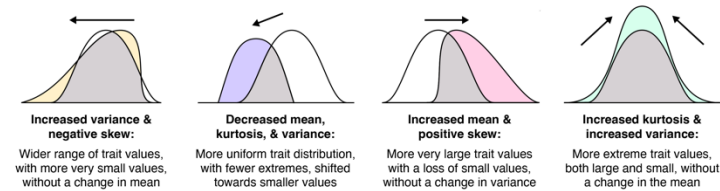
## Simple shifts in trait distributions

A shift in a single moment of the trait distribution does not necessarily correspond to shifts in other moments. For example, the mean value can remain stable while changes at the distributional tails alter the trait community.



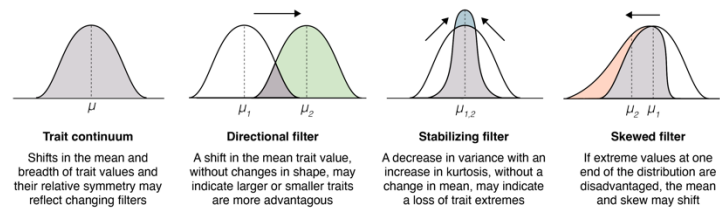
## Shifts across multiple trait distribution dimensions

Complex changes in trait distributions involve concurrent alterations in several moments. Understanding how combinations of these moments change can reveal which trait values are gained or lost within a population.

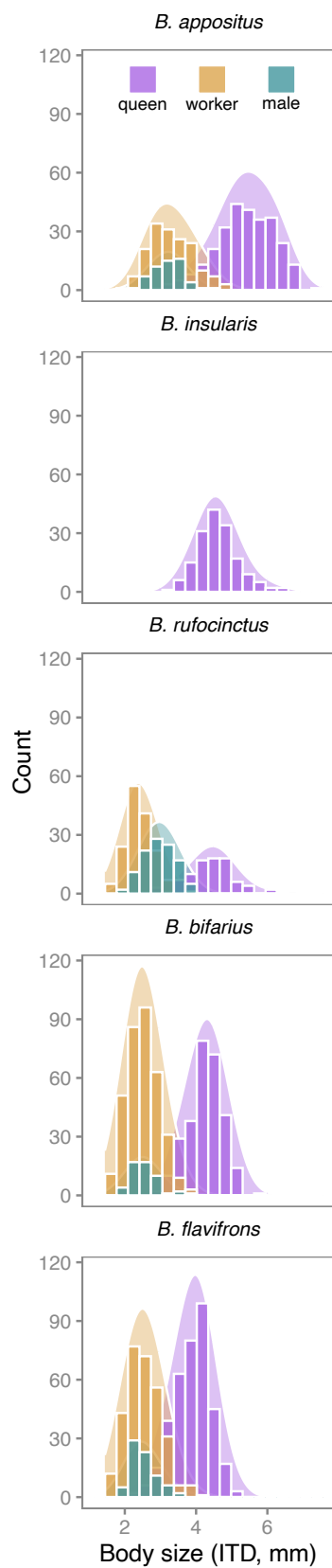


## Hypothetical filtering processes shifting trait distributions

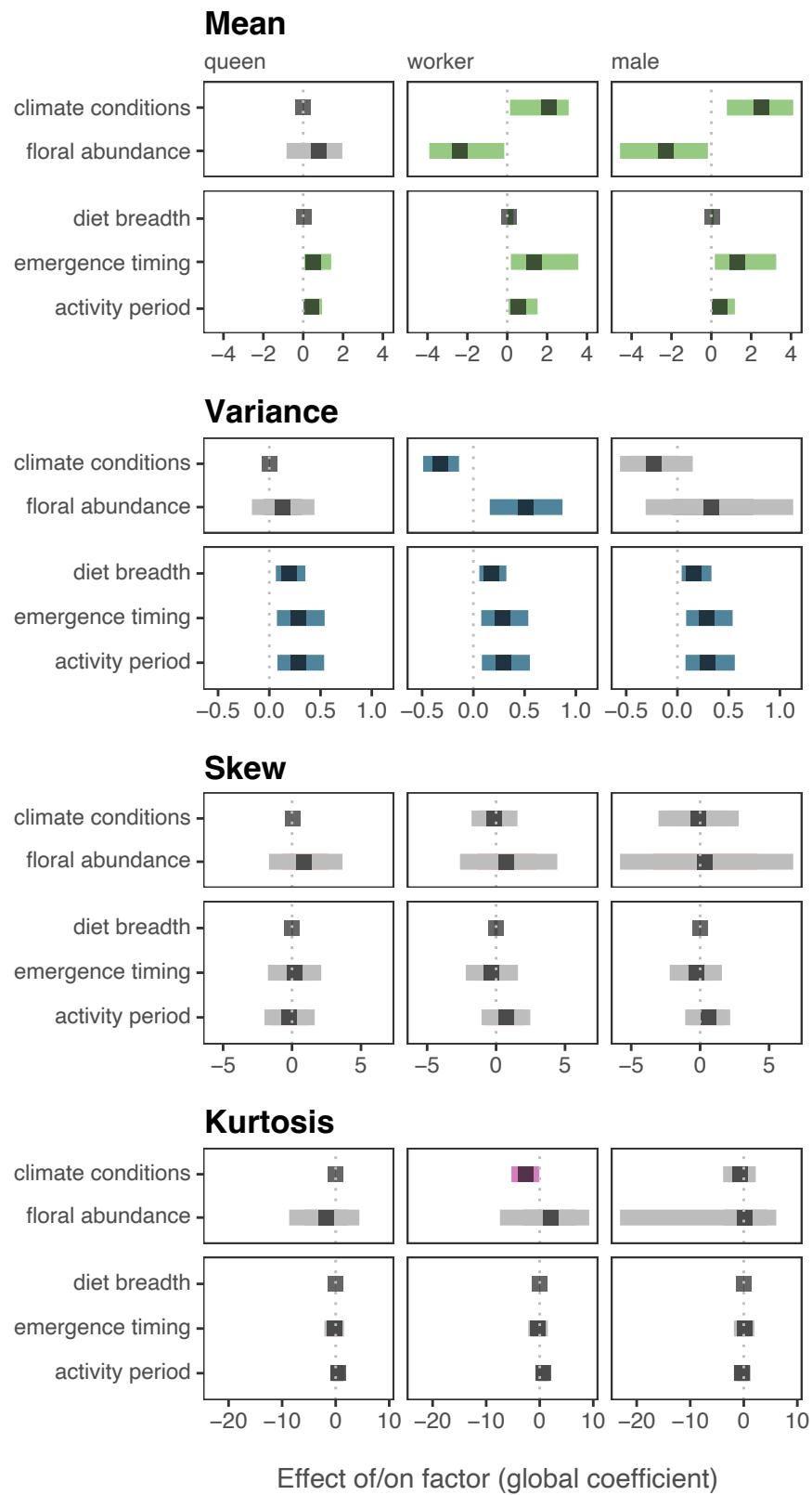
The distribution of traits in a population is maintained by both phenotypic plasticity and local adaptation, which filter trait values admitted by changing abiotic and biotic conditions.



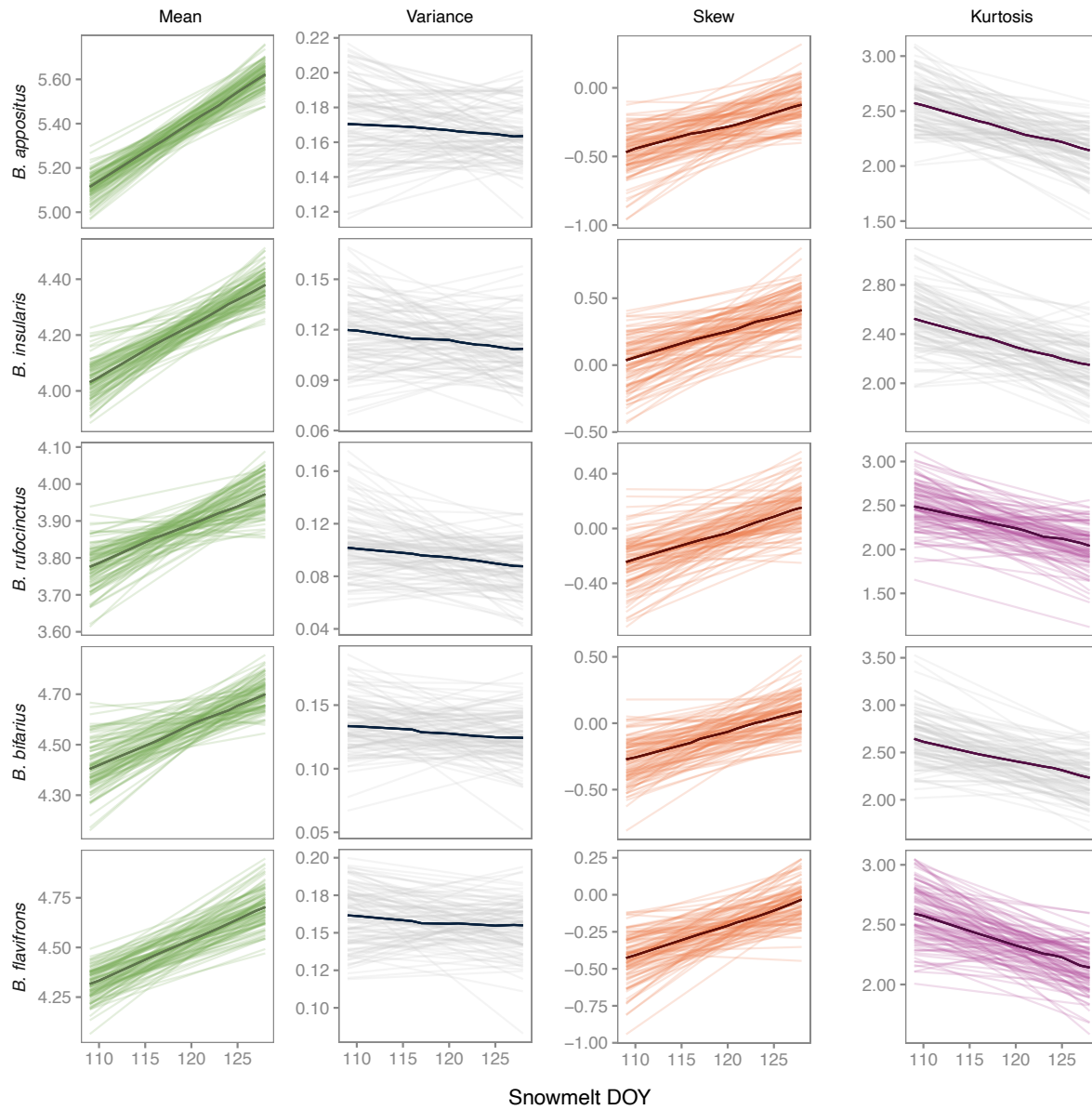
**Box 2.1.** The distribution of traits in a population can be described by several measures – mathematical moments – representing its central tendency, variation around the mean, symmetry on either side of the mean, and the concentration of extreme values around the mean. Shifts in one or several of these measures can reveal which trait values are gained or lost in a population. Changes in the mean and variance may also be accompanied by changes in the skewness and kurtosis of the trait distribution, which reflect environmental filtering of extreme trait values at the distributional tails. This filtering framework represent ecological analogs of classic evolutionary processes.



**Figure 2.1.** Histogram of the spread of bumble bee body sizes among castes and across species, highlighting the characteristic bimodal distribution of larger queens and smaller workers, with males as a subset of worker sizes. On average, workers are more variable in size than queens, followed by males. Species are ordered by descending queen size; ITD is intertegular distance.

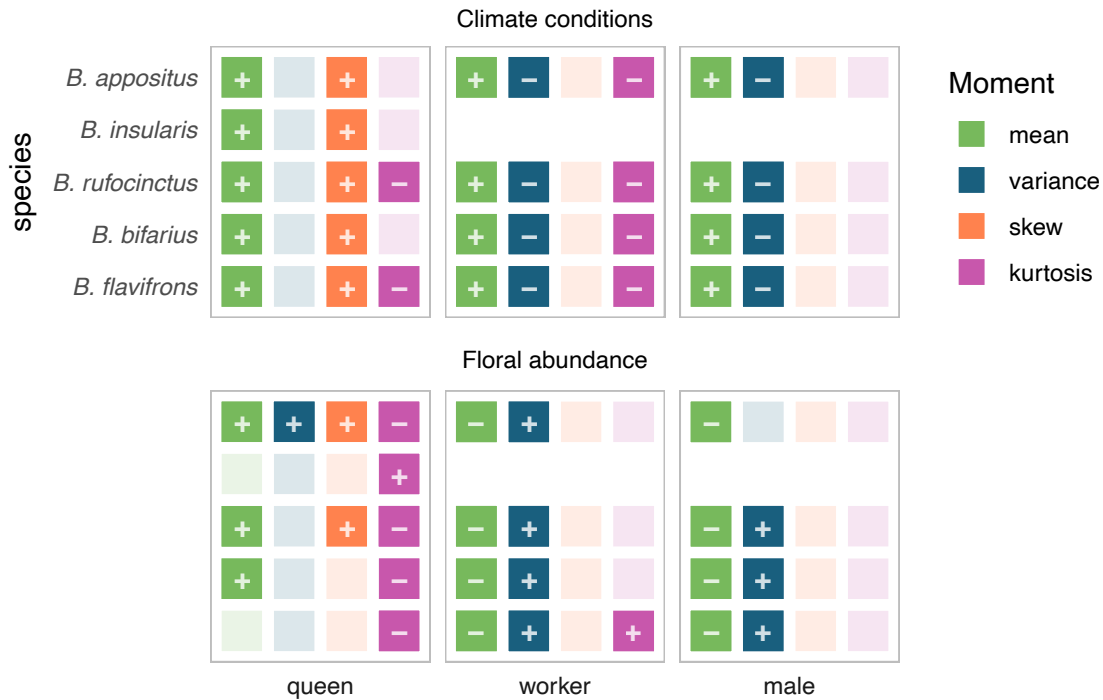


**Figure 2.2.** The global effects of climate conditions and floral abundance on bumble bee body size distributional moments, and the effects of body size distributions on bumble bee diet breadth and two measures of phenology: emergence timing and activity period. Points represent the median estimate (i.e., the effect size) of the posterior distribution of the model, error bars represent the 95<sup>th</sup> credible interval (CI) of the estimate for mean size and 85<sup>th</sup> CI for higher moments. Coloured points and bars indicate evidence of a strong non-zero effect. For queens, the effect of climate conditions represents a degree change in a body size distributional moment per day change in spring snowmelt, and for floral abundance, the effect size is change per 10 flowers in the previous year. For workers and males, climate conditions represent the ratio of temperature to precipitation during their seasonal activity window, and floral abundance the change per 10 flowers during their developmental period in the current year. Diet breadth is measured as standardized Hurlbert's niche breadth, emergence timing is the day of year by which 5% of the population has emerged, and activity period is the number of days between emergence and peak activity. There were strong but mixed global effects on and of mean and variance across caste, with no strong evidence of an effect on or of skew, whereas the kurtosis (i.e., evenness) of worker body size was strongly influenced by climate.

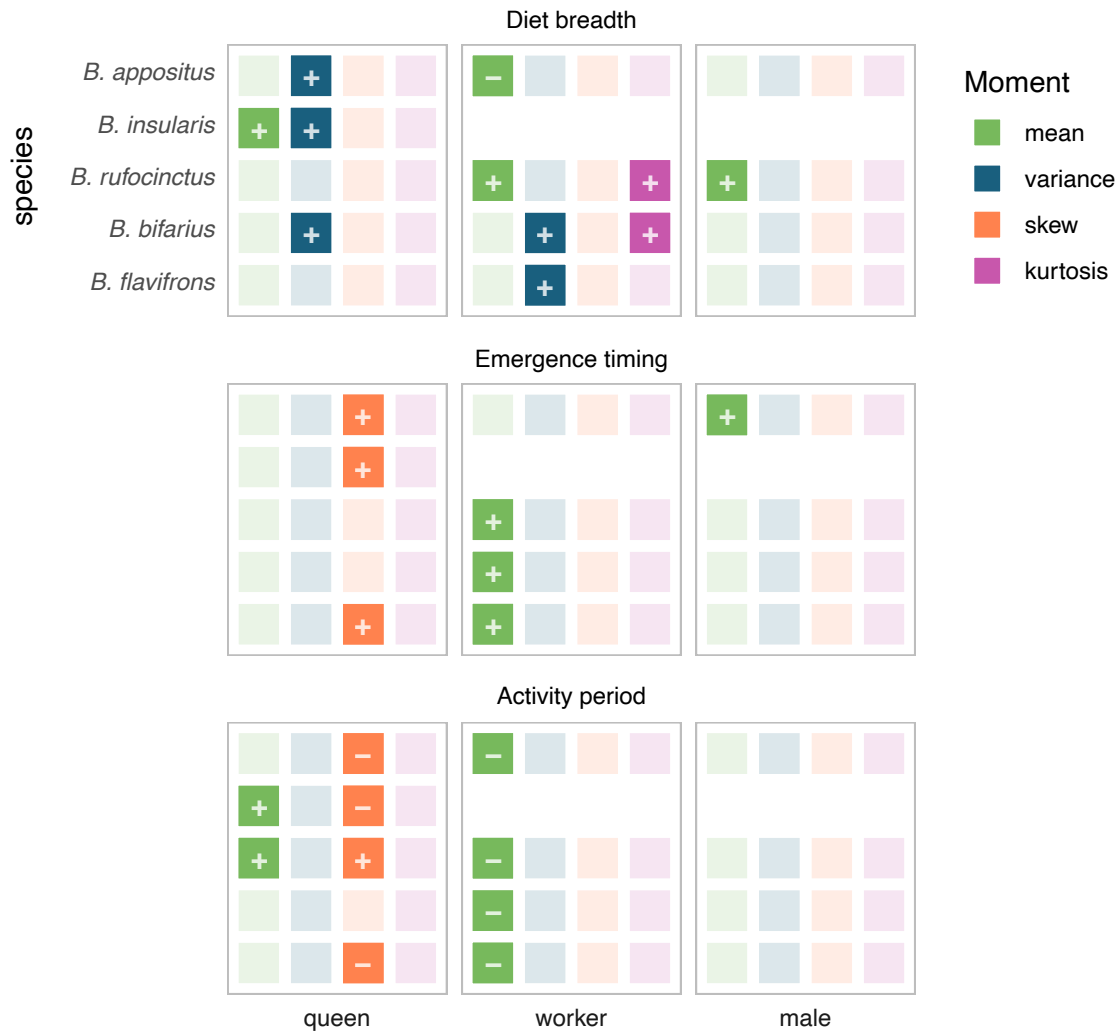


**Figure 2.3.** Conditional effects of snowmelt timing day of year (DOY) on the body size distributional moments of queens across species. With earlier snowmelt, queens across all species declined in mean size and exhibited negative skew, with two species showing increased kurtosis. In other words, earlier snowmelt led to a higher frequency of small-bodied queens with an increase in extremely small individuals. Model fit lines represent 100 draws from the posterior distribution of a Bayesian linear mixed effect model for each distributional moment, with species as a random effect. Coloured lines indicate

evidence of an effect from the full model at the 95th credible interval (CI) for mean size and 85<sup>th</sup> CI for higher moments. Species are ordered by descending queen size.



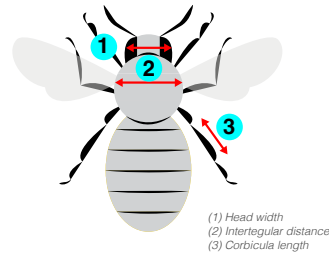
**Figure 2.4.** Summary of the conditional effects of climate and floral resources on bumble bee body size distributional moments. Each grouped grid represents a set of models (see Figure 3), where any highlighted squares indicate evidence of a correlation at the 95<sup>th</sup> credible interval (CI) for mean and 85<sup>th</sup> CI for higher moments, with the direction of the relationship (positive [+], or negative [-]). Each subheading represents a driver of trait variation, each column represents a caste (queen, worker, male), and each row within a group represents a species, ordered by descending queen size. There were strong effects of both climate and floral resources on body size across all distributional moments, with idiosyncratic effects across species and caste. See supplement for full models. Results are absent for *Bombus insularis* workers as this kleptoparasitic species does not produce them and for males as our sample size was less than 30 individuals.



**Figure 2.5.** Summary of the conditional effects of body size distributions on bumble bee diet breadth and two measures of phenology, emergence timing and activity period. Each grouped grid represents a set of models (see Figure 3), where any highlighted squares indicate evidence of a correlation at the 95<sup>th</sup> credible interval (CI) for mean and 85<sup>th</sup> CI for higher moments, with the direction of the relationship (positive [+], or negative [-]). Each subheading represents an effect of trait variation, each column represents a caste (queen, worker, male), and each row within a group represents a species, ordered by descending queen size. There were strong effects of body size across distributional moments, with idiosyncratic effects across species and caste. See supplement for full models. Results are absent for

*Bombus insularis* workers as this kleptoparasitic species does not produce them and for males as our sample size was less than 30 individuals.

## Focal traits



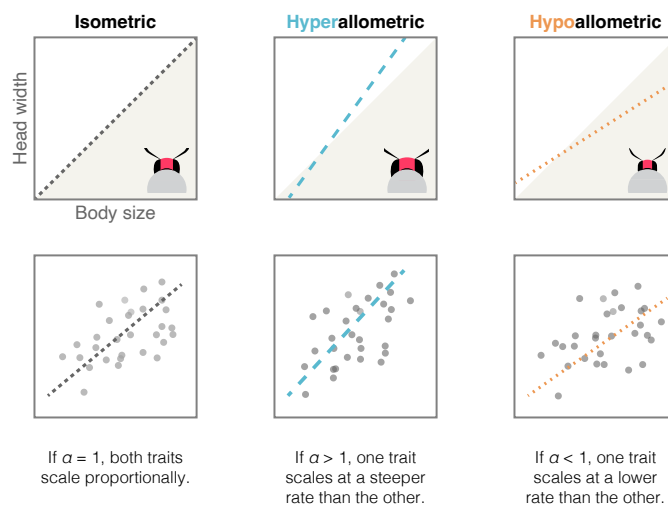
Morphological relationships across an organism can be described between pairs of traits and among sets of traits.

For two traits, their scaling relationship can be described by the coefficient  $\alpha$ .

For 2+ traits, the integration among the set can be described through the variance in a correlation matrix:  $Var(\lambda)$ .

## Trait scaling

Trait scaling ( $\alpha$ ) can be characterized with a Standardized Major Axis (SMA) approach. In contrast to an linear regression, SMAs calculate  $\alpha$  through centroid of the data cloud from two interchangeable axes and account for variance in both variables.



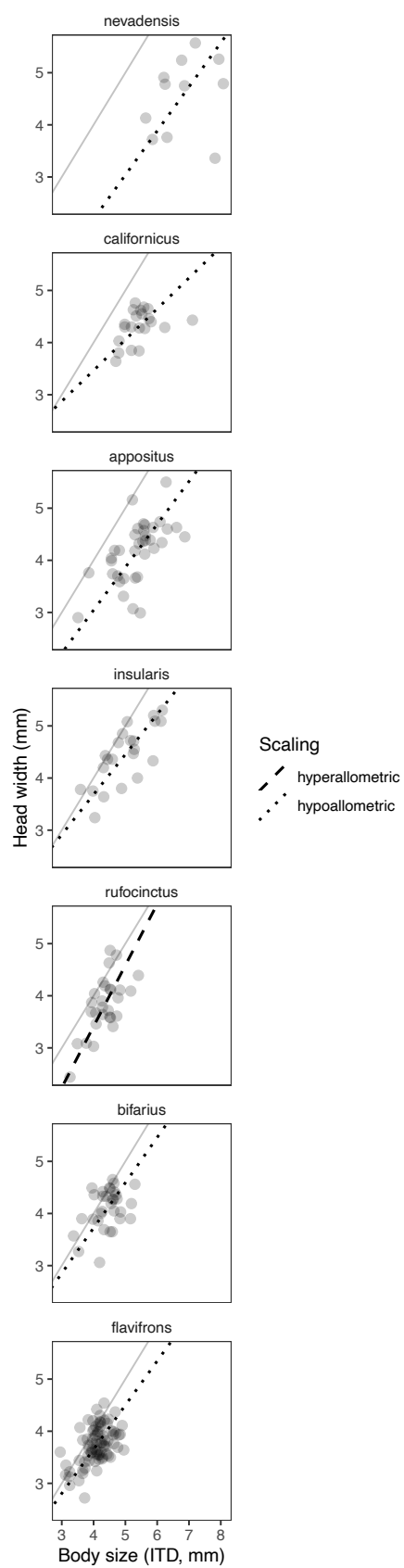
## Trait integration

The propensity of a set of traits to scale in a coordinated manner is called morphological integration. These coordination patterns can be identified from the degree of variance across a correlation matrix:  $Var(\lambda)$ .

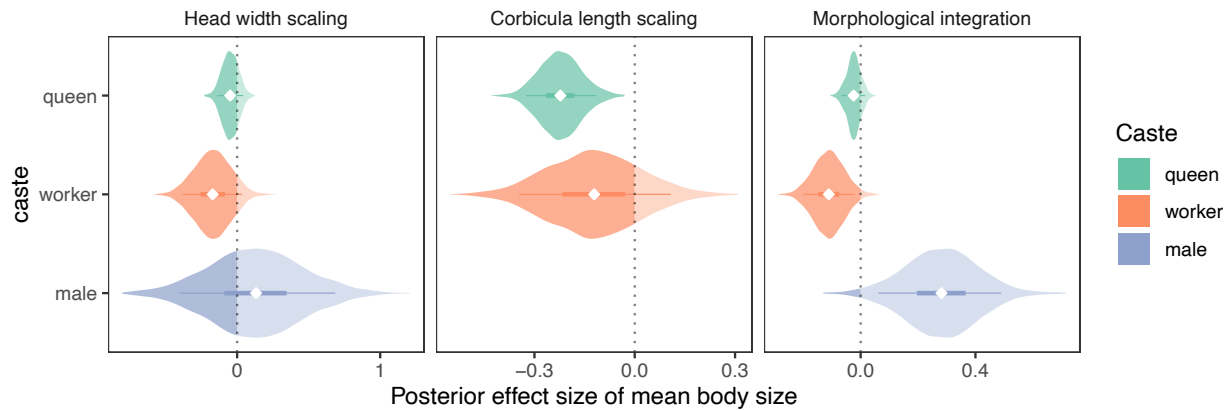
This variance can be relativized across matrices so that  $Var(\lambda)$  values span 0 to 1, where 1 indicates complete integration and 0 no integration. For example, if all traits scale with the same  $\alpha$ , they would be perfectly integrated:  $Var(\lambda) = 1$ .



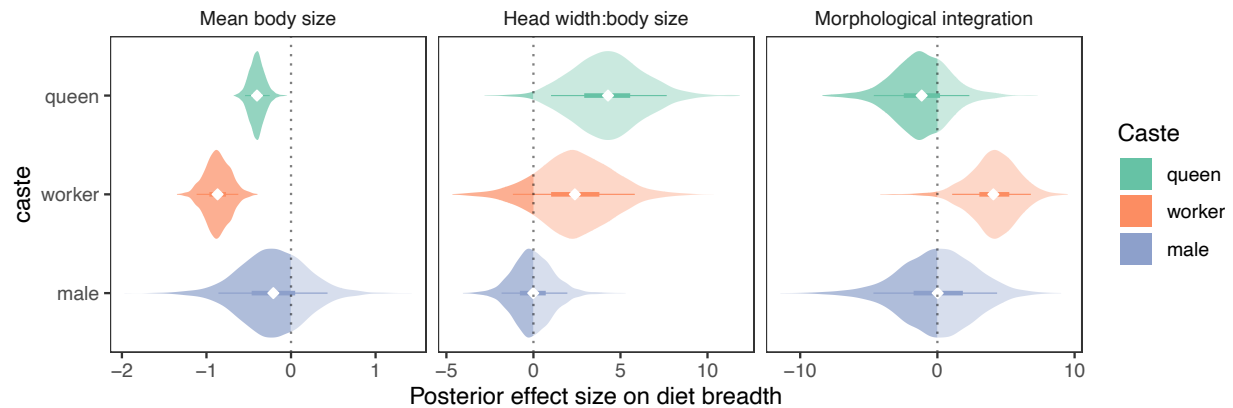
**Figure 3.1.** Conceptual outline for our trait covariation approach, using bumble bees as our study species. The relationships among morphological traits can be described between pairs of traits (scaling) and across sets of traits (integration). Scaling relationships reflect the change in one trait given a change in another, while the degree of integration across three or more traits reflect the propensity of the group of traits to covary together.



**Figure 3.2.** Scaling relationships between head width and body size (intertegular distance, ITD) among queens across species. Each panel represents data from the most abundant sampling unit (site-year combination) for each species, ordered from largest mean size to smallest. Points represent individual bees. The 1:1 solid grey line represents hypothetical isometry. Scaling is estimated from standardized major axis models, and linetype corresponds to the scaling coefficient  $a$ :  $a > 1$  = hyperallometric,  $a < 1$  = hypoallometric.



**Figure 3.3.** Model effect sizes of mean body size (intertergular distance, ITD) and its relation to trait scaling coefficients (i.e., head width and corbicula length) and trait covariation (i.e., morphological integration) by caste. Colored violins represent the posterior density distribution, with darker shading indicating estimates below zero. White points represent the mean of the prediction, with the outer thinner band showing the 90% credible interval (CI) and the inner thicker band showing the 50% (CI). As mean body size increases, scaling relationships in female bees become increasingly hypoallometric, i.e., larger queens and workers have proportionally smaller heads and corbicula. For queens and workers, morphological integration decreased with increasing body size while in males, increasing body size was associated with greater integration.



**Figure 3.4.** Model effect sizes of the relationships between diet breadth (estimated as Hill-Shannon diversity at 95% coverage) and mean body size (intertegular distance, ITD), head width scaling (i.e., relative brain size), and morphological integration across castes. Colored violins represent the posterior density distribution, with darker shading indicating estimates below zero. White points represent the mean of the prediction, with the outer thinner band showing the 90% credible interval (CI) and the inner thicker band showing the 50% (CI). As mean body size increases, diet breadth decreases across all castes. As relative head width increases, workers and queens have broader diets. As the degree of morphological integration increases, worker diet breadth increases.

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## APPENDIX

**Supporting Information:** Chapter 1

**Journal:** Environmental Entomology

**Title:** Ecological drivers and consequences of bumble bee body size variation

**DOI:** <https://doi.org/10.1093/ee/nvac093>

**Authors:** Jacquelyn L. Fitzgerald<sup>1,2,3</sup>, Jane E. Ogilvie<sup>3</sup>, and Paul J. CaraDonna<sup>1,2,3</sup>

**Authors Institutions:**

<sup>1</sup> Plant Biology and Conservation, Northwestern University, Evanston, IL 60201, USA

<sup>2</sup> Negaunee Institute for Plant Conservation Science & Action, Chicago Botanic Garden, Glencoe, IL 60022, USA

<sup>3</sup> Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA, 81224

**Supplementary Materials:**

The supplementary materials for the literature review in Chapter 1 include detailed metadata on the included studies, search strategies, and data extraction processes. These materials are accessible via the publisher's platform:

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**Supporting Information:** Chapter 2**Journal:** Journal of Animal Ecology**Title:** Intraspecific body size variation across distributional moments reveals trait filtering processes**DOI:** <https://doi.org/10.1111/1365-2656.14186>**Authors:** Jacquelyn L. Fitzgerald<sup>1,2,3</sup>, Jane E. Ogilvie<sup>3</sup>, and Paul J. CaraDonna<sup>1,2,3</sup>**Authors Institutions:**<sup>1</sup> Plant Biology and Conservation, Northwestern University, Evanston, IL 60201, USA<sup>2</sup> Negaunee Institute for Plant Conservation Science & Action, Chicago Botanic Garden, Glencoe, IL 60022, USA<sup>3</sup> Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA, 81224**Supplementary Materials:**

The supplementary materials for the study in Chapter 2 include comprehensive data, analyses, and figures supporting the findings presented in this chapter, which are too extensive to include directly in this dissertation. The supplementary files are accessible through the publisher's platform and are detailed as follows:

**Citation:** Fitzgerald, Jacquelyn L., Jane E. Ogilvie, and Paul J. CaraDonna. "Intraspecific body size variation across distributional moments reveals trait filtering processes." *Journal of Animal Ecology* (2024).

Supplementary data file available at: [10.1111/1365-2656.14186](https://doi.org/10.1111/1365-2656.14186)

Supplementary Files:

**Figure S2.1.** The relationship between skewness and kurtosis of a distribution through the inequality ( $K \geq \beta S^2 + \alpha$ ). Figure S2. Body size mean, variance, skew, and kurtosis, with standard error, across bumble bee species and caste.

**Table S2.1.** Linear model describing the inequality relationship between skew and kurtosis ( $K \geq \beta S^2 + \alpha$ ).

**Table S2.2.** Global effects of climate conditions (snowmelt timing, mid-, and late-season temperature:precipitation ratios) on body size distributional mean, variance, skew, and kurtosis for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

**Table S2.3.** Conditional effects of climate conditions (snowmelt timing, mid-, and late-season temperature:precipitation ratios) on body size at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

**Table S2.4.** Effect of floral resource conditions on body size distributional mean, variance, skew, and kurtosis for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

**Table S2.5.** Conditional effects of floral resource abundance on body size at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

**Table S2.6.** Global effects of body size distributional mean, variance, skew, and kurtosis on diet breadth for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

**Table S2.7.** Conditional effects of body size on diet breadth at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

**Table S2.8.** Global effects of body size distributional mean, variance, skew, and kurtosis on emergence timing for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

**Table S2.9.** Conditional effects of body size on emergence timing at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

**Table S2.10.** Global effects of body size distributional mean, variance, skew, and kurtosis on phenological activity period for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

**Table S2.11.** Conditional effects of body size on phenological activity period at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

## Supporting Information: Chapter 3

**Table S3.1.** Mean and variation of focal traits within each species and caste. ITD is intertegular distance, CV is the coefficient of variation  $c_v = \frac{\sigma}{\mu}$ .

| Species                | Caste  | Mean ITD (mm) | CV ITD | Mean head width (mm) | CV head width | Mean corbicula length (mm) | CV corbicula length | N   |
|------------------------|--------|---------------|--------|----------------------|---------------|----------------------------|---------------------|-----|
| <i>B. appositus</i>    | queen  | 5.35          | 0.15   | 4.11                 | 0.13          | 4.67                       | 0.14                | 263 |
|                        | worker | 3.3           | 0.18   | 2.91                 | 0.18          | 3.17                       | 0.18                | 153 |
|                        | male   | 3.15          | 0.11   | 2.94                 | 0.16          | NA                         | NA                  | 30  |
| <i>B. bifarius</i>     | queen  | 4.26          | 0.12   | 3.75                 | 0.12          | 4                          | 0.14                | 275 |
|                        | worker | 2.51          | 0.18   | 2.35                 | 0.18          | 2.41                       | 0.18                | 338 |
|                        | male   | 2.53          | 0.12   | 2.53                 | 0.12          | NA                         | NA                  | 21  |
| <i>B. californicus</i> | queen  | 5.5           | 0.13   | 4.24                 | 0.11          | 4.65                       | 0.11                | 101 |
|                        | worker | 2.95          | 0.19   | 2.78                 | 0.23          | 2.83                       | 0.21                | 14  |
| <i>B. flavifrons</i>   | queen  | 3.88          | 0.14   | 3.53                 | 0.13          | 3.86                       | 0.14                | 360 |
|                        | worker | 2.53          | 0.19   | 2.36                 | 0.18          | 2.47                       | 0.19                | 302 |
|                        | male   | 2.48          | 0.14   | 2.48                 | 0.14          | NA                         | NA                  | 62  |
| <i>B. insularis</i>    | queen  | 4.66          | 0.12   | 4.23                 | 0.11          | NA                         | NA                  | 146 |
| <i>B. nevadensis</i>   | queen  | 7.14          | 0.13   | 4.81                 | 0.13          | 5.38                       | 0.16                | 34  |
|                        | worker | 4.3           | 0.11   | 3.21                 | 0.11          | 3.66                       | 0.14                | 21  |
| <i>B. rufocinctus</i>  | queen  | 4.44          | 0.14   | 3.81                 | 0.12          | 4.15                       | 0.12                | 69  |
|                        | worker | 2.4           | 0.16   | 2.28                 | 0.16          | 2.32                       | 0.18                | 142 |
|                        | male   | 3.02          | 0.14   | 2.81                 | 0.13          | NA                         | NA                  | 92  |

**Table S3.2.** Model estimates for the relationship between the scaling slope of head width to mean body size from a Bayesian model with caste as an interactive effect. As mean body size increased, the scaling relationship of head width became more hypoallometric in queens and workers. The table presents credible intervals at multiple confidence levels, arranged with lower bounds (l\_) in ascending order (50% to 99%) followed by upper bounds (u\_) in descending order (99% to 50%). This arrangement allows readers to trace the expanding width of credible intervals from the median estimate. Cells are color-coded to aid interpretation: yellow indicates credible intervals that cross zero, while blue indicates intervals that do not cross zero, providing a visual guide to the strength and certainty of the relationships.

| Caste  | Estimate | l_0.5 | l_0.6 | l_0.7 | l_0.8 | l_0.9 | l_0.95 | l_0.99 | u_0.99 | u_0.95 | u_0.9 | u_0.8 | u_0.7 | u_0.6  | u_0.5 |
|--------|----------|-------|-------|-------|-------|-------|--------|--------|--------|--------|-------|-------|-------|--------|-------|
| queen  | -0.05    | -0.09 | -0.1  | -0.11 | -0.12 | -0.14 | -0.16  | -0.20  | 0.09   | 0.06   | 0.04  | 0.02  | 0.01  | -0.001 | -0.01 |
| worker | -0.17    | -0.26 | -0.28 | -0.31 | -0.34 | -0.38 | -0.42  | -0.49  | 0.16   | 0.07   | 0.03  | -0.01 | -0.04 | -0.06  | -0.09 |
| male   | 0.13     | -0.09 | -0.14 | -0.21 | -0.29 | -0.4  | -0.50  | -0.69  | 0.97   | 0.77   | 0.69  | 0.55  | 0.47  | 0.41   | 0.35  |

**Table S3.3.** Model estimates for the relationship between the scaling slope of corbicula length to mean body size from a Bayesian model with caste as an interactive effect. As mean body size increased, the scaling relationship of corbicula became more hypoallometric, with the strongest relationship in queens. Male bumble bees do not have corbicula. The table presents credible intervals at multiple confidence levels, arranged with lower bounds (l\_) in ascending order (50% to 99%) followed by upper bounds (u\_) in descending order (99% to 50%). This arrangement allows readers to trace the expanding width of credible intervals from the median estimate. Cells are color-coded to aid interpretation: yellow indicates credible intervals that cross zero, while blue indicates intervals that do not cross zero, providing a visual guide to the strength and certainty of the relationships.

| Caste  | Estimate | l_0.5 | l_0.6 | l_0.7 | l_0.8 | l_0.9 | l_0.95 | l_0.99 | u_0.99 | u_0.95 | u_0.9 | u_0.8 | u_0.7 | u_0.6 | u_0.5 |
|--------|----------|-------|-------|-------|-------|-------|--------|--------|--------|--------|-------|-------|-------|-------|-------|
| queen  | -0.22    | -0.27 | -0.28 | -0.29 | -0.3  | -0.33 | -0.34  | -0.39  | -0.06  | -0.09  | -0.12 | -0.14 | -0.16 | -0.17 | -0.18 |
| worker | -0.12    | -0.22 | -0.24 | -0.27 | -0.3  | -0.35 | -0.39  | -0.46  | 0.23   | 0.15   | 0.11  | 0.06  | 0.02  | -0.01 | -0.03 |

**Table S3.4.** Model estimates for the relationship between overall morphological integration to mean body size from a Bayesian model with caste as an interactive effect. As mean body size increased, queens and workers exhibited less integration, while males became more integrated. The table presents credible intervals at multiple confidence levels, arranged with lower bounds (l\_) in ascending order (50% to 99%) followed by upper bounds (u\_) in descending order (99% to 50%). This arrangement allows readers to trace the expanding width of credible intervals from the median estimate. Cells are color-coded to aid interpretation: yellow indicates credible intervals that cross zero, while blue indicates intervals that do not cross zero, providing a visual guide to the strength and certainty of the relationships.

| Caste  | Estimate | l_0.5 | l_0.6 | l_0.7 | l_0.8 | l_0.9 | l_0.95 | l_0.99 | u_0.99 | u_0.95 | u_0.9 | u_0.8 | u_0.7 | u_0.6  | u_0.5 |
|--------|----------|-------|-------|-------|-------|-------|--------|--------|--------|--------|-------|-------|-------|--------|-------|
| queen  | -0.02    | -0.04 | -0.04 | -0.05 | -0.06 | -0.07 | -0.08  | -0.09  | 0.04   | 0.02   | 0.02  | 0.01  | 0.001 | -0.004 | -0.01 |
| worker | -0.11    | -0.15 | -0.16 | -0.17 | -0.18 | -0.2  | -0.22  | -0.25  | 0.04   | -0.01  | -0.02 | -0.04 | -0.06 | -0.07  | -0.07 |
| male   | 0.28     | 0.28  | 0.2   | 0.18  | 0.15  | 0.12  | 0.06   | 0.03   | -0.05  | 0.63   | 0.53  | 0.49  | 0.44  | 0.41   | 0.39  |

**Table S3.5.** Model estimates for the relationship of mean body size to diet breadth from a Bayesian model with caste as an interactive effect. As mean body size increased, diet breadth decreased in queens and workers. The table presents credible intervals at multiple confidence levels, arranged with lower bounds (l\_) in ascending order (50% to 99%) followed by upper bounds (u\_) in descending order (99% to 50%). This arrangement allows readers to trace the expanding width of credible intervals from the median estimate. Cells are color-coded to aid interpretation: yellow indicates credible intervals that cross zero, while blue indicates intervals that do not cross zero, providing a visual guide to the strength and certainty of the relationships.

| Caste  | Estimate | l_0.5 | l_0.6 | l_0.7 | l_0.8 | l_0.9 | l_0.95 | l_0.99 | u_0.99 | u_0.95 | u_0.9 | u_0.8 | u_0.7 | u_0.6 | u_0.5 |
|--------|----------|-------|-------|-------|-------|-------|--------|--------|--------|--------|-------|-------|-------|-------|-------|
| queen  | -0.40    | -0.46 | -0.48 | -0.49 | -0.51 | -0.54 | -0.57  | -0.63  | -0.14  | -0.21  | -0.25 | -0.29 | -0.31 | -0.33 | -0.35 |
| worker | -0.87    | -0.97 | -0.99 | -1.02 | -1.06 | -1.12 | -1.15  | -1.26  | -0.48  | -0.57  | -0.62 | -0.68 | -0.71 | -0.74 | -0.77 |
| male   | -0.21    | -0.47 | -0.53 | -0.61 | -0.69 | -0.86 | -1.01  | -1.30  | 0.86   | 0.58   | 0.43  | 0.29  | 0.19  | 0.11  | 0.05  |

**Table S3.6.** Model estimates for the relationship of head width scaling to diet breadth from a Bayesian model with caste as an interactive effect.

As head scaling increased (i.e., proportionally larger brains), diet breadth strongly increased in queens and moderately increased in workers. The table presents credible intervals at multiple confidence levels, arranged with lower bounds (l\_) in ascending order (50% to 99%) followed by upper bounds (u\_) in descending order (99% to 50%). This arrangement allows readers to trace the expanding width of credible intervals from the median estimate. Cells are color-coded to aid interpretation: yellow indicates credible intervals that cross zero, while blue indicates intervals that do not cross zero, providing a visual guide to the strength and certainty of the relationships.

| Caste  | Estimate | l_0.5 | l_0.6 | l_0.7 | l_0.8 | l_0.9 | l_0.95 | l_0.99 | u_0.99 | u_0.95 | u_0.9 | u_0.8 | u_0.7 | u_0.6 | u_0.5 |
|--------|----------|-------|-------|-------|-------|-------|--------|--------|--------|--------|-------|-------|-------|-------|-------|
| queen  | 4.24     | 2.92  | 2.59  | 2.18  | 1.72  | 1.01  | 0.53   | -0.76  | 10.02  | 8.41   | 7.66  | 6.92  | 6.37  | 5.92  | 5.56  |
| worker | 2.35     | 1.02  | 0.66  | 0.25  | -0.34 | -1.18 | -1.92  | -3.44  | 8.2    | 6.68   | 5.82  | 5.12  | 4.56  | 4.16  | 3.79  |
| male   | -0.08    | -0.78 | -0.94 | -1.15 | -1.43 | -1.83 | -2.26  | -3.04  | 3.75   | 2.5    | 1.95  | 1.47  | 1.14  | 0.9   | 0.71  |

**Table S3.7.** Model estimates for the relationship of morphological integration to diet breadth from a Bayesian model with caste as an interactive effect. As the degree of integration increased, diet breadth increased in workers. The table presents credible intervals at multiple confidence levels, arranged with lower bounds (l\_) in ascending order (50% to 99%) followed by upper bounds (u\_) in descending order (99% to 50%). This arrangement allows readers to trace the expanding width of credible intervals from the median estimate. Cells are color-coded to aid interpretation: yellow indicates credible intervals that cross zero, while blue indicates intervals that do not cross zero, providing a visual guide to the strength and certainty of the relationships.

| Caste  | Estimate | l_0.5 | l_0.6 | l_0.7 | l_0.8 | l_0.9 | l_0.95 | l_0.99 | u_0.99 | u_0.95 | u_0.9 | u_0.8 | u_0.7 | u_0.6 | u_0.5 |
|--------|----------|-------|-------|-------|-------|-------|--------|--------|--------|--------|-------|-------|-------|-------|-------|
| queen  | -1.16    | -2.45 | -2.79 | -3.2  | -3.75 | -4.63 | -5.54  | -7.25  | 4.73   | 3.28   | 2.33  | 1.38  | 0.9   | 0.51  | 0.19  |
| worker | 4.16     | 3.06  | 2.73  | 2.34  | 1.81  | 1.08  | 0.31   | -1.66  | 8.42   | 7.34   | 6.81  | 6.23  | 5.83  | 5.51  | 5.24  |
| male   | 0.1      | -1.73 | -2.17 | -2.67 | -3.37 | -4.66 | -5.82  | -8.18  | 6.74   | 5.08   | 4.35  | 3.44  | 2.73  | 2.32  | 1.86  |