



Selection on size variation: more variation in bumble bee workers and in the wild

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Abstract

Body size is a key feature of any organism, influencing almost every aspect of its life history. Social insects provide an interesting model to study body size, because they often exhibit a high degree of worker size variation within the colony. Size variation is often studied in the lab, sometimes using commercially purchased colonies; therefore, it is important to test if the size variation found in the lab is representative of natural conditions. Furthermore, the distribution of worker sizes within a colony is generally assumed to be adaptive at the colony level. However, such size variation may also result from poor control over brood development (and weak selection on the trait). Using bumble bee (*Bombus impatiens*), which display a large amount of worker size variation when raised in the lab, we tested whether (1) workers from lab colonies with commercial queens are more variably sized than workers from field colonies with wild queens, and (2) whether workers are more variably sized than concurrently raised males or queens. We found that the size variation was greater in field than lab colonies, and workers varied more than either reproductive caste. Our results indicate that the amount of variation produced is accessible to selection, possibly actively regulated by nurse behavior. These results also suggest that size variation is not a lab artifact and is common across both laboratory and natural environments. Therefore, evolutionary and ecological implications of size variation can be inferred from lab-reared colonies with consideration for even greater size variation.

Keywords Body size · Variation · Bumble bee · Commercial · Lab artifact

Introduction

Body size is one of the most striking and significant traits of all organisms as it relates to many ecological and physiological features, including an organism's metabolism, fecundity, and survival rate (Brown et al. 2004). Size is often under strong selection (Kingsolver and Pfennig 2007), and local conditions can create differences in size among populations (Chown and Gaston 2010). A classic example is Bergmann's rule which describes the pattern of larger average body sizes at colder temperatures owing to heat conservation (Bergmann 1847; Blanckenhorn and Demont 2004; Geraghty

et al. 2007). While originally intended to describe differences among species, studies have expanded Bergmann's rule to explain variation in average size among populations within a species (Ashton 2002). Intraspecific variation in body size may also result from constraints and life-history trade-offs (Fox and Czesak 2000; Roff 1993). Much of the work on how ecological factors influence body size variation has focused on solitary organisms (Roff 1993), despite a long history of examining body size variation within social insects (Oster and Wilson 1978; Reviewed in Wills et al. 2018; Wilson 1953).

Social insects provide some of the most spectacular examples of intraspecific size variation. Bumble bees (*Bombus* spp.), a longstanding model organism for behavior, ecology, and evolution, exhibit an approximately tenfold variation in mass among the full-sister workers within the same colony (Goulson 2003). Previous studies on body size in bumble bees have recorded average sizes (Grab et al. 2019; Knee and Medler 1965; Persson and Smith 2011; Sutcliffe and Plowright 1988), but rarely measured within-colony size variation from wild colonies (however, see Plowright

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and Jay 1968). When size variation is recorded, it is often from foragers (Austin and Dunlap 2019; Peat et al. 2005a), a small, size-biased subset of the workers (Brian 1952; Goulson et al. 2002), and mixes individuals from different colonies which are known to differ in average size (Couvillon et al. 2010). A bumble bee worker's size is determined by food uptake during development (Pendrel and Plowright 1981; Plowright and Jay 1968), but the variation in size of workers within a colony is associated with internal (Shpigler et al. 2013) and external factors (Kelemen and Dornhaus 2018). Mechanistically, the size variation within a bumble bee colony is generated by nurse workers feeding developing workers on the periphery less food (Couvillon and Dornhaus 2009; Pereboom et al. 2003; Plowright and Jay 1968; Sutcliffe and Plowright 1988). However, higher temperatures and reduced forage availability can induce greater size variation within a colony (Kelemen and Dornhaus 2018; Kelemen et al. 2020). This plasticity means artificial environments (i.e., a laboratory) may produce size variation that differs from that found in nature. Furthermore, many bumble bee colonies used in experiments are commercially purchased (Cnaani and Hefetz 1994; Herrmann et al. 2018; Jandt and Dornhaus 2014; Kelemen and Dornhaus 2018). These may have a history of artificial selection (Beekman et al. 2000; Ings et al. 2006), leading to potentially further differences between the size variation of lab colonies and field colonies.

In social insects, the constraints and life history trade-offs on size likely differ from solitary organisms due to the reproductive division of labor between the queen and worker castes. Workers no longer need to invest in traits for mating, dispersal, and reproduction. Instead, their size and variation in size are thought to be under selection at the colony level to improve colony maintenance, survival, and reproduction (Oster and Wilson 1978; Powell 2009). However, in bumble bees, it is currently unclear if the degree of size variation itself (as opposed to any particular average size) has any function (Cnaani and Hefetz 1994; Herrmann et al. 2018; Jandt and Dornhaus 2014). Alternatively, variation may exist not, because it is adaptive per se, but because the colony has not evolved a way to reduce it, either because of a constraint or relaxed selection on size. If size variation is due to a constraint, such as a lack of a mechanism to regulate feeding rates across individual brood, we would expect that all castes (workers, virgin queens, and males) produced within the colony should vary similarly in body size when reared concurrently. If size variation is only generated in some but not other castes, it suggests a mechanism to regulate size variation exists, which should be accessible to natural selection. In this case, the size distribution differences between castes may be adaptive.

We compared the size variation produced by field- and lab-reared colonies to test the hypothesis that commercial colonies reared in the lab generate size variation that exceeds

that found in wild colonies. We compared the size variation among concurrently reared worker and reproductive castes to test the hypotheses that colonies possess a mechanism to regulate the amount of variation produced in a particular caste.

Methods

Field vs. lab colonies

We obtained six colonies, hereafter referred to as lab colonies, of *Bombus impatiens* from Koppert Biological Systems (Howell, MI, USA.) in 2015 and maintained them in the lab. We housed them in wooden nest boxes (38 cm × 23 cm × 8 cm) lined with pine cat litter (Nature's Earth Products, Inc., West Palm Beach, FL, U.S.A.) to reduce moisture and covered with transparent Plexiglas. Colonies were kept under laboratory conditions (12: 12 h light:dark cycle; 25 ± 1 °C; ~35% humidity) at the University of Arizona, Tucson, U.S.A. environmental conditions they were assigned to (see below). The colonies were provided with 50% sugar solution and pollen (fresh frozen and ground, obtained from Koppert) ad libitum. Once colonies started producing queens, at the start of the reproductive stage, the colonies were frozen.

We reared eleven colonies, hereafter referred to as field colonies, of *B. impatiens* from wild queens in Erving, Massachusetts in 2017 and 2018. Foraging queens were collected from private residences on flowering crabapple (*Malus* spp.) during the month of May. To reduce the incidence of queens who may have already established nests, only those without pollen in corbicula were used in rearing. Using modified protocols from Skyrms (2011), queens were established in plastic starter boxes (16.5 cm × 10 cm × 4 cm) with screened ventilation holes and acrylic covers to facilitate feeding. Queens were kept under controlled environmental conditions of humidity (55–65%), temperature (28 °C ± 5 °C) and under constant red light (250 W heat lamps) photoperiod.

To stimulate egg production, queens were provided with two (2) compressed wax cells (Mann Lake, Hackensack, MN) affixed inside a supplemental egg cup (16 oz Dart insulated foam cup bottom) and regional Spring pollen collected fresh from honey bee colonies and stored frozen (Autumn Morning Farm Beekeeping Supplies, Barre, MA) (Skyrms 2011). One compressed wax cell was situated upright and filled with sugar water, and the other was inverted to emulate a typical *Bombus* spp. pupae. Sugar syrup and pollen were provided directly to queens within starter boxes. Pollen was provided as loose granules (0.4 g daily) and as a ball mixed with sugar syrup and covered in wax (Mann Lake, Hackensack, MN). Sugar syrup (Pro-Sweet Liquid Feed, Mann

Lake, Hackensack, MN) was provided using modified portion cups (Dixie 3.25 oz clear souffle cup). Queens were given fresh pollen daily for the first five (5) days after introduction into a starter box. Those queens that did not initiate egg laying within the first five (5) days were released back to the area of capture. After colony initiation (i.e., queen laid eggs), fresh pollen and sugar syrup feeders were provided weekly until field placement.

Colonies were selected for field placement after reaching a minimum size of 10 workers, all stages of brood (i.e., egg clumps, larval clusters, and pupae), and a queen. Prior to field placement, colonies were relocated to larger, wooden nest boxes (25.4 cm × 21.6 cm × 19.1 cm) and provided with a piece (10.16 cm × 2.54 cm × 10.16 cm) of organic raw cotton fiber (Walmart, Bentonville, AR) to use as an involucrum. Colonies were placed in the field in the same locations as they were queen collected. Colonies were left in the field for the duration of the summer. After colonies produced queens, at the end of the reproductive stage, the colonies were frozen. These colonies were allowed to produce queens to minimize this study's impact on the natural bumble bee population.

After the nests were frozen, we separated all the (now empty) pupal cases—pupal cases from all individuals raised in a bumble bee colony remain in the nest and are not reused by bees; they thus provide a record of the sizes of all individuals reared over the entire colony life. We measured each pupal case's diameter with digital calipers to the nearest 0.1 mm at its widest horizontal diameter (Neiko Tools, USA). Pupal cases are a good proxy for the size of the adults that emerge from them (Couvillon and Dornhaus 2009), as each pupating bumble bee larva spins its own case. We measured pupal cases to capture the total size variation produced by each colony, not just the size variation of the current worker cohort. The sex of individuals produced cannot be determined from the pupal cases. However, the number of males produced was low. Weekly newly emerged bees were marked with non-toxic paint pens, and only two lab colonies produced males (0.8% and 1% of total individuals produced). We distinguished workers from queens based on their relative size, as the distribution of pupal case sizes was bimodal (S1 Fig). Therefore, we categorized pupal cases with less than 11 mm diameter as workers. The average colony size of field (39 ± 44 worker pupal cases) colonies was substantially smaller than that of lab colonies (478 ± 163 worker pupal cases).

Workers vs. males vs. queens

We obtained eleven colonies of *B. impatiens* from Kopert Biological Systems ($n=4$) and Biobest (Romulus, MI, USA; $n=7$) in 2017 and 2018. These colonies were housed in similar conditions as the previous colonies.

Weekly we measured the thorax width (a standard measure of body size in bumble bees (Goulson 2003)) of all newly emerged individuals with digital calipers to the nearest 0.1 mm. We used data only from workers, males, and virgin queens produced concurrently within the colonies to control for potential confounding factors such as colony size and colony age. We did this, because the purpose of this comparison was to see if larvae from the different castes are raised to attain different degrees of variation, not to get an overall measure of worker variation as in the previous experiment.

Male *B. impatiens* are morphologically distinct from females and could be categorized based on these traits (the most distinctive trait is yellow hair on the face in males). The distribution of female thorax widths was again bimodal (S2 Fig) with minimal overlap between workers and queens. We classified females as workers or queens based on body size, cohort demography, and behavior. Individuals below 6.25 mm were considered workers and above this size were considered queens, except for one individual above 6.25 mm, as it was produced in a female cohort of (otherwise) all workers, and it did not leave the nest but remained, performing tasks in the nest, thus showing worker-like behavior.

Analysis

Statistical analyses were conducted using R 3.2.5 (R Development Core Team 2013), and linear mixed models were conducted using the package nlme (Pinheiro et al. 2017). If the size variation differed between field and lab colonies, a model where the variance (i.e., variation in sizes) could differ should better fit the data. We built two linear mixed models with pupal case width as the response factor, *colony* as a random factor, and *environment* as a fixed factor. One model allowed for heterogeneous variances in size between the environments using the weight function (varIdent) (Zuur et al. 2009). The other model had equal variances in size. We tested for differences in model fit using a log-likelihood test. In addition, we used the best fit model to test if the average pupal case width differed between environments. We performed a power analysis on our results using nlmeU (Galecki et al. 2015). We followed the same methods to compare the size variation among workers, males, and virgin queens (i.e., the castes), except the linear models used *caste* as a fixed factor.

We verified the underlying assumptions of these linear mixed models by visually inspecting their residuals following Zuur et al. (2009), and no transformations were necessary.

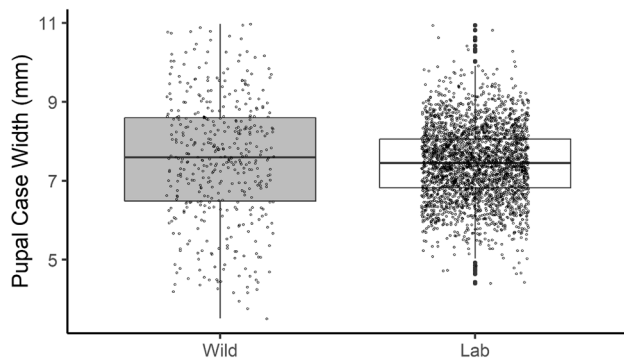


Fig. 1 Pupal case width in wild (426 cases) and lab (2867 cases) colonies of *B. impatiens*. The line in the box represents the median. The box represents the interquartile range. The whiskers represent the maximum and minimum values. The filled circles represent the outliers. The open circles show the raw data

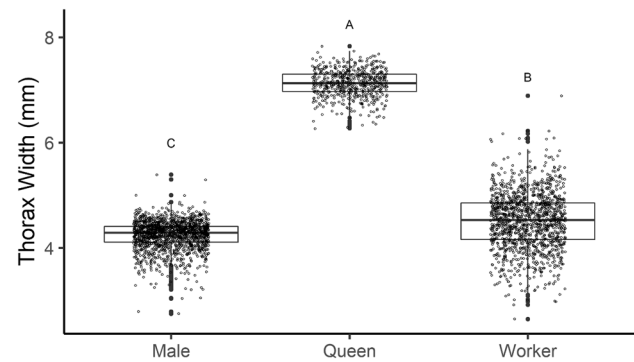


Fig. 2 Thorax widths of males ($n=1547$), queens ($n=563$), and workers ($n=1359$) concurrently produced in *B. impatiens* colonies. The line in the box represents the median. The box represents the interquartile range. Letters represent statistical significance among castes. The whiskers represent the maximum and minimum values. The filled circles represent the outliers. The open circles show the raw data

Results

More worker size variation in field colonies

Field- and lab-reared colonies did not differ in their average pupal case width ($t_{15}=0.51$, $p=0.61$) (Fig. 1, Table S1). With our sample size, we had the power to detect a difference as small as 9.7% between the two groups at the conventional 80% power (Cohen 1992). However, there was greater variation in pupal case width from field colonies (estimated model heterogeneity coefficient of field colonies = 1.84 and lab colonies = 1.00; $L_1=335.75$, $p<0.001$; ΔAICc between models >3 Table S2). Field colonies had 73% more variation in pupal cases width (7.54 ± 1.56 mm) than lab colonies (7.44 ± 0.90 mm).

Workers show more size variation than other castes even when produced concurrently

Worker had larger thorax widths than males ($t_{3456}=-14.80$, $p<0.001$), but smaller thorax widths than virgin queens ($t_{3456}=123.20$, $p<0.001$) (Fig. 2, Table S3). Worker thorax widths were more variable than those of concurrently reared males or virgin queens (estimated model heterogeneity coefficient worker = 2.04, male = 1.00, and queen = 0.95; $L_2=843.18$, $p<0.001$; ΔAICc between models >3 Table S4). Worker had 97% more variation in thorax width (4.51 ± 0.53 mm) than males (4.24 ± 0.27), and 107% more variation than virgin queens (7.12 ± 0.26).

Discussion

We found that workers of colonies reared in the lab with commercial queens were not more variable than field colonies with wild queens. In fact, the workers of field colonies were more variable in size than those of lab colonies. This clearly demonstrates that the high degree of size variation documented in the literature from colonies with commercial queens and often studied in the lab (Cnaani and Hefetz 1994; Couvillon and Dornhaus 2009; Herrmann et al. 2018; Jandt and Dornhaus 2014; Kelemen and Dornhaus 2018) is a natural phenomenon, and appears not to be an artifact of these artificial conditions.

Lab and field colonies differed not only in their environment but also their genetic makeup and either of these factors may explain why field colonies were more variable in size. Commercial colonies of *Bombus terrestris* are better nectar foragers than wild counterparts (Ings et al. 2006). This increase in foraging ability is attributed to their larger size. However, we found no difference between the average size in commercial and field colonies of *B. impatiens*. Similar to studies in *B. terrestris*, we found that commercial colonies produced more workers prior to gyne production (Gösterit and Gürel 2005; Ings et al. 2006). In our study, lab colonies were fed *ad-lib*, while field colonies had to forage on local floral resources. This difference in resources is likely to have contributed to the larger colony size (higher number of individuals) of the lab colonies; it may also contribute to the worker size or size variation produced (Kelemen et al. 2020). Regardless, the fact that the size variation in the lab colonies did not exceed that of natural colonies means that size variation is not an artifact of either artificial selection or artificial rearing conditions.

We also found that there was greater size variation among workers than among males or virgin queens. This result suggests that bumble bee colonies can control the body size variation of any caste they produce, and thus supports the hypothesis that size variation within workers is a result of adaptive evolution: either selection on workers to be variable (Couvillon and Dornhaus 2010; Goulson et al. 2002), or relaxed selection on size uniformity on workers compared to queens and males (del Castillo et al. 2012; Inoue 2011; Owen 1988). In either case, worker size variation is thus not merely a ‘constraint’ inaccessible to selection.

Our estimate of worker size variation is a conservative estimate, because we used the data only from the workers that were produced, while males or virgin queens were being produced. We did that to control for potential confounding factors such as colony size and colony age. The social environment influences the size of workers produced within a colony, such that a higher number of workers produce larger average workers (Shpigler et al. 2013). Average worker size and size variation has been found to change throughout the season, but the direction of change is not consistent across colonies (Couvillon et al. 2010; Knee and Medler 1965; Peat et al. 2005b). These changes through time mean that the size variation we observed by examining workers only at a single timepoint is likely less than if we included all the workers the colonies produced in this study. However, we still found significantly higher size variation among workers within colonies despite the developing workers, males, and virgin queens being intermingled throughout the same nest, experiencing the same social environment, and being fed by the same workers. Caste-specific differences in feeding frequencies result from differences in development (Pereboom et al. 2003), and our results suggest that these rules vary in frequency and uniformity among castes.

In conclusion, our study suggests that the phenotypic diversity among workers in bumble bee colonies observed in the lab is not an artifact. Therefore, it is appropriate to infer the evolutionary and ecological implications of size variation from lab-reared colonies. Even so, wild colonies exhibit greater size variation than lab colonies, which is important to consider that the benefit of size variation to the colony may only be exhibited at these more extreme size variations. In addition, our study suggests that bumble bees possess mechanisms to regulate size variation, and therefore, that size variation among workers is accessible to selection and thus the outcome of evolution.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00040-022-00850-y>.

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