

Body size variation in bees: regulation, mechanisms, and relationship to social organization

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Size polymorphism is common in bees, and is determined by environmental factors such as temperature, brood cell size, and the diet provided to developing larvae. In social bees, these factors are further influenced by intricate interactions between the queen, workers, and the developing brood which eventually determine the final size and caste of developing larvae. Environmental and social factors act in part on juvenile hormone and ecdysteroids, which are key hormonal regulators of body size and caste determination. In some social bees, body size variation is central for social organization because it structures reproductive division of labor, task allocation among workers, or both. At ecological scales, body size also impacts bee-mediated pollination services in solitary and social species by influencing floral visitation and pollination efficacy.

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Many animals show intra-specific variation in body size. In some cases, there appear to be benefits of having a larger body size. For example, size is positively associated with improved performance, competitiveness, and capacity to monopolize resources such as territory or mates in some animals [1], and has a strong association with female fecundity in insects [2]. Larger individuals can also better contend with some abiotic environmental conditions. For example, larger-sized individuals are better able to maintain sufficient body temperatures in colder environments and are therefore more likely to be found at higher latitudes and altitudes, a phenomenon known as Bergmann's rule [3]. However, given that large individuals require a larger investment in terms of energy and

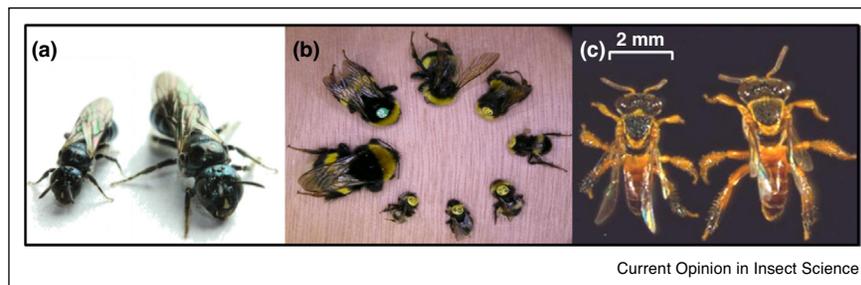
resources, parents are presented with a trade-off between investing in fewer, larger offspring or more, smaller ones [4,5,1]. Moreover, a larger body size is not always more advantageous. For example, in hotter climates, smaller body sizes and larger surface area to volume ratios promote heat loss and cooling by evaporation [6]. Where there is a genetic basis to size variation, it may evolve by local adaptation, or by fluctuating (e.g. different body sizes are favored in different years or seasons) or frequency-dependent (i.e. frequency-dependent mating success or predation of individuals of a certain body size) selection. The ultimate forces influencing size-related fitness intersect with the underlying proximate mechanisms that generate body size variation. These proximate mechanisms are varied, but across disparate animal taxa often involve diet and the conserved role of nutritional pathways, including the insulin and target of rapamycin (TOR) pathways [7,8], among other mechanisms. Relationships between size and fitness are thus complex, and body size distributions are shaped by natural selection and plastic responses to the environment.

The broader proximate [7] and ultimate [9] mechanisms that shape insect body size have been extensively reviewed elsewhere. Here, we focus specifically on recent insights into drivers and consequences of intraspecific body size variation in bees (Apoidea: Anthophila). Variation in the body size of bees (Figure 1) can be found at many levels: In both social and solitary species, considerable variation is found within and between populations, and in social species, size variation is also found within and between colonies [10,11]. Size variation in bees may affect their pollination services, and in social species contributes to their social organization.

Ecological drivers of size variability in bees

As in other holometabolous insects, bee body size is determined during the larval stage, and is strongly influenced by the environment. For example, experimental studies have demonstrated that nest microclimate during early development influences adult body size in the managed solitary species *Osmia bicornis* [12] and *Megachile rotundata* [13]. At broader ecological and evolutionary scales, there are additional associations between abiotic factors such as temperature and bee body sizes. Most bee species studied so far show increases in size with increasing latitude or altitude. This pattern follows Bergmann's rule, which is common but not universal in insects, and is likely shaped by evolutionary processes [10,14*,15,9]. Seasonal changes in temperature and day length also

Figure 1



Body size variation in bees.

(a) Body size variation in the facultatively social small carpenter bee *Ceratina calcarata*, between a small worker-like subordinate daughter (left) and a dominant reproductive mother (right) (photo credit Sandra Rehan). (b) Size polymorphism within a bumble bee (*Bombus terrestris*) colony. The queen is the largest individual to the left, and all other bees are sister workers that may vary in body mass by up to 10-fold (photo credit Shai Yerushalmi). (c) Worker forager (Left) and guard (Right) of the stingless bee *Tetragonisca angustula*. Guards are 30% heavier than foragers (from Ref. [30**]).

drive differences in insect body sizes, including in bees [12,9,16–18].

Biotic factors also contribute to intraspecific body size variation. Bees depend overwhelmingly on floral resources for food, and the abundance and composition of these resources, which change across habitats and seasons, are important determinants of larval diet. In bees, as in other insects, diet regulates development and terminal body size, with the general rule that smaller larval provisions generate smaller-bodied bees (described in greater detail in Section ‘Proximate mechanisms underlying body size variation’). There are also consequences of body size that influence how bees extract food resources from their environments. Body size is typically positively associated with foraging range [19] and the amount of pollen and nectar load the bee can carry [20,21,22**]. Therefore, smaller-sized individuals might be more prevalent in areas with fewer food resources, whereas larger sizes may be advantageous in habitats where there is a greater need to forage at greater distances, or maximize individual foraging loads [23]. However, being large is not always advantageous. Larger individuals may suffer higher parasitism rates or be preferentially targeted by some predators, for example in the case of conopid fly host selection [24]. There is also evidence suggesting that smaller-sized bumble bees exhibit higher survival under some conditions [22**,25].

Given the importance of ecological factors in shaping body size, it is perhaps not surprising that recent studies have demonstrated that global changes, such as habitat degradation and land use change, may be driving changes in bee body size distributions towards smaller sizes. For example, in a study of a ground nesting andrenid (*Andrena nasonii*), Renauld *et al.* [26] found more smaller-sized bees in areas of greater agricultural intensification. There is also evidence that over the last century and a half, some

bee species have become smaller [27] and that larger-bodied bee species are more likely to have exhibit declines in relative abundance [28]. The underlying mechanistic drivers of these directional shifts in bee body size distributions have not been explicitly studied, but are likely related to the same aforementioned environmental drivers that generate fluctuations in body size variation. For example, in degraded or rapidly changing habitats there are often trends towards fewer floral resources, which might lead to smaller pollen masses provisioned in larval cells, which is directly related to final body size in bees (see below Section ‘Proximate mechanisms underlying body size variation’). This is corroborated by recent studies on flowering habitat enhancement as a method for buffering this body size decline [29*].

Proximate mechanisms underlying body size variation

Solitary bees

Most of the world’s bee species are solitary and typically have limited ability to actively regulate their nest environment. Like other holometabolous insects, all bees go through several larval molts, with the final one resulting in development into a pupa. Given that pupae do not feed, the final mass of the last larval instar usually determines adult size. Research, mostly with fruit flies (i.e. *Drosophila melanogaster*) and moths (*Manduca sexta*), indicates that body size is largely determined by growth rate and the duration of sensitive periods during larval growth, although in some species variation in the number of instars may also play a role. These key developmental features are orchestrated by multiple regulatory processes affecting cell growth and proliferation (reviewed in Ref. [9]). Bees have been relatively little explored in this regard, but given the overall similarity between moths and flies, there is currently no reason to assume that the organization principles determining body size in bees are significantly different, although the details may vary.

Food amount and quality are considered among the most important factors controlling body size in both solitary and social bees [20,31–34]. In insects, diet impacts growth rate, which in turn affects instar size [9]. The microenvironment, and specifically the temperature during larval growth, is also important [35–37]; Figure 2). Studies with moths and other insects have shown that temperature has a positive effect on growth rate, and on the rate of biochemical reactions, such as JH clearing, which affects the time of pupation [9]. In mass provisioning solitary species, brood size is limited by the size of the cell and the quality or quantity of the food the mother deposits in the cell before she lays the egg. This maternal control is perhaps best exemplified in recent studies showing that in solitary mason bees (*Osmia* spp.), pupation is triggered when larvae consume all pollen in the maternally provided provision, rather than when they reach a critical weight [38,39]. In small carpenter bees (genus *Ceratina*), the first daughter is fed with less food and a distinct diet composition, and is smaller-bodied relative to her later sisters [40]. However, it is unknown whether the mother explicitly controls the diet provision for the first cell, or whether its distinct provision simply reflects seasonal changes in floral resource availability. Studies with honey bees in which the effect of cell size and food provisioned were uncoupled suggest that both factors are important in this species, but it is yet not clear how information about cell-size are detected and processed to affect the larval developmental program [37].

In progressively provisioning species, nursing adults dynamically control the diet of developing larvae and can respond to hunger signals from the brood (see below Section ‘The control of larval diet by tending adults’). Interactions between tending adults and larvae have been studied mostly in social insects (discussed below, Section ‘Social bees’), but similar mechanisms are also found in some solitary wasps and may also apply for solitary bees [41].

Social bees

The control of larval diet by tending adults

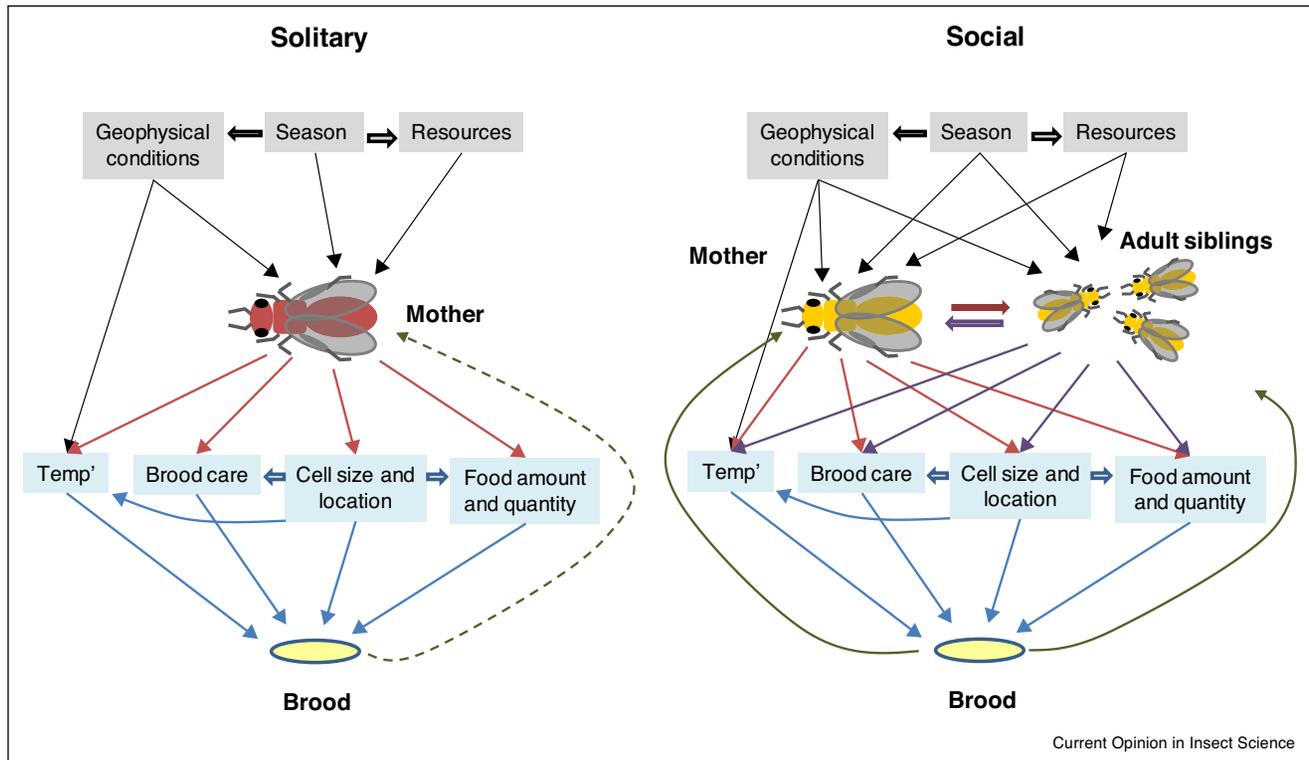
In social bees, complex interactions between the queen, workers, and developing brood determine larval diet and environment, which in turn influence development and final size (Figure 2, right). In progressive provisioners, tending adults dynamically control larval diet and feeding schedule. The most iconic manifestation of diet-related control over development in social insects is in the case of royal jelly of honey bees (*Apis mellifera*), which determines whether a larva develops into a (larger) queen or a worker [42]. Royal jelly contains proteins known as ‘Major Royal Jelly Proteins’ (MRJPs), as well as additional bioactive molecules that are produced in the head glands of nurse workers and affect regulatory processes controlling larval development [37,43–46]. For example, a remarkable recent finding is that MRJP-3 acts as an extracellular

RNA binding protein that facilitates the transfer of RNAs from workers to larvae [47]. There is also evidence suggesting that phytochemicals and small RNAs present in pollen, which is only fed to worker-destined larvae, influence development and caste fate in honey bees [48,49]. The nine MRJPs of the honeybee evolved from a single progenitor gene encoding a member of the ancient Yellow protein family. The two sequenced bumble bees genomes encode only a single MRJP, suggesting that the expansion of this protein family in bees is specific to honey bees [50]. There is currently no evidence for qualitative differences between regurgitate fed to worker-destined versus queen-destined larvae in bumble bees [51]. However, there is evidence that direct contact with the queen impacts larval developmental duration in *Bombus terrestris*, which is consistent with the notion that the queen transfers some currently undescribed pheromones and/or other nutritional or bioactive molecules to larvae (Shpigler *et al.* [52], Figure 3). Interestingly, there is evidence that dietary honey bee royal jelly can affect development and body size in non-*Apis* insects, such as *Drosophila* [43] and bumble bees (Bloch, unpublished results). This suggests that some aspects of the regulatory architecture of body size determination are shared between these lineages, even if upstream drivers (e.g. royal jelly) differ.

Rearing environment

Similar to solitary bees and other insects, larval development and the terminal body size of social bees is sensitive to the environment. In social bees, these factors are further influenced by interactions between the queen, workers, and developing brood. The sum of these factors is often referred to as the ‘social environment’ which also includes colony age/size. Social bees can tightly regulate many aspects of the nest microenvironment that impact brood development and body size (Figure 2, right panel). For example, honey bees thermoregulate their nests to $35 \pm 0.5^\circ\text{C}$ and have strong control over other factors such as humidity and CO₂ levels [42]. The location of larvae in the nest has been shown to affect body size in the bumble bee *Bombus impatiens* [53] and in the stingless bee *Tetragonisca angustula* [54] and can be an important source for within-colony variation in body size. Larvae in the center of the brood comb are fed more frequently, but they may also benefit from improved thermoregulation compared with brood developing at the comb periphery (but see Kelemen and Dornhaus [16] for a study suggesting that thermoregulation is similar in the center and periphery of colonies of the bumble bee *B. impatiens*). In some bumble bees, average worker size increases with colony age in a way that is consistent with increasing food availability or brood care with colony growth (Figure 3) [55–57,52]. A cross-fostering experiment in *B. terrestris*, exchanging larvae between young and old colonies, demonstrated that these effects are driven by the rearing colony environment, rather than factors in the egg [52]. Thus, body

Figure 2



A summary of the factors affecting body size in solitary and social bees.

Body size variation depends on environmental conditions that affect the brood ambient condition (e.g. temperature) and food amount and quality. In both solitary and social bees, resource availability and the size and position of the larval cell may influence offspring size. In social bees, a complex interplay between the queen, the workers, and the brood ('the social environment') determine the ambient conditions, location, cell size, and the diet provisioned to the developing larva, which together determine its final body size and caste fate. Not all arrows are applicable to all species and their relative importance may vary with species ecology and life history traits.

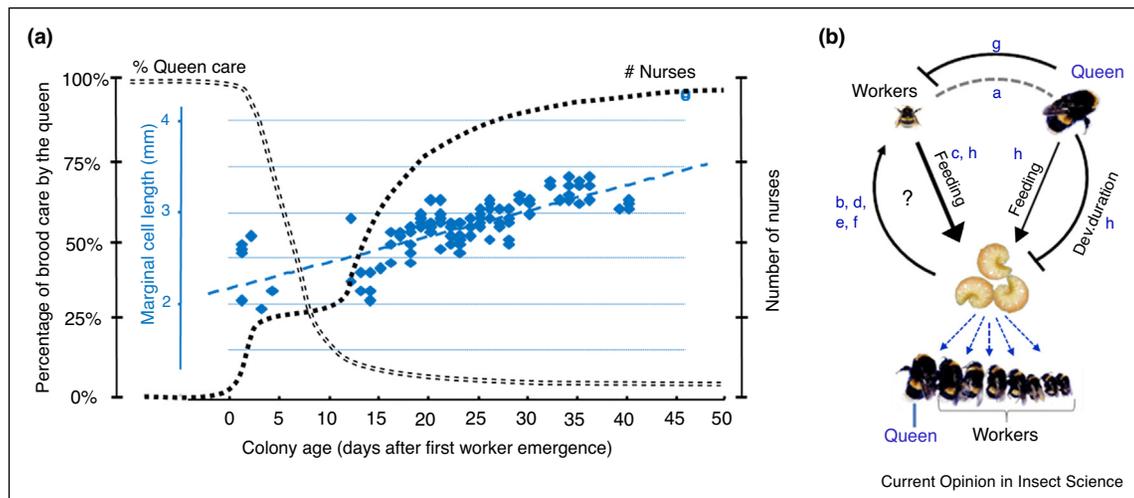
size variation can originate from spatial or temporal variation in resource distribution and, more generally, brood care among the larvae. In addition to the location of the larvae, this distribution can also be affected by the ratio of nurse bees to larvae, and according to the task repartition with other duties needed, such as foraging or thermoregulation, depending on colony growth and geophysical conditions [36,35,12,37,31,16,17].

Interactions with tending adults that affect body size

Both the queen and the workers may control the larval diet and quality of care, and this can be influenced by interactions between these parties and with the brood. For example, in honey bee colonies, group size and queen pheromones affect the nurse worker decision of whether to feed female larvae with queen or worker jelly [42]. There is also evidence that larvae in social species communicate their needs to tending adults. For example, in bumble bees, cuticular pheromones can inform about larval hunger state [58**], although tending workers can vary in their response threshold or motivation to respond to this signal [59]. The volatile honey bee brood pheromone E- β -ocimene also appears to function as a hunger

signal, inducing workers to tend brood cells and feed larvae [60**]. However, the interests of developing brood and adults may differ. Nursing adults allocate their limited resources between multiple developing or future brood, rather than optimizing food availability for a single larva. In addition, adults may act in specific ways that limit the size of the developing larvae. An interesting example comes from *Polistes* paper wasps, in which adults produce mechanical signals that modulate larval development and reduce propensity to develop into larger gynes [61,62]. Social inhibition seems to also be important in the bumble bee *B. terrestris*. In this species larvae tended by the queen pupate earlier, are commonly smaller, and are less likely to develop into gynes, compared with larvae reared by only workers [52**,63]. Queen inhibition is mediated, at least partially, by direct contact with the queen, and is compromised in larvae separated from her by a queen excluder [52**]. As colony group sizes grow larger, more workers are available to care for the larvae, and the probability that larvae will be tended by the queen decreases (Figure 3a). The increase in worker number further affects queen behavior, as she reduces brood feeding and increases egg laying, which may

Figure 3



A schematic self-organized model for the increase in worker size as a function of colony age in the bumble bee *Bombus terrestris*. The model is based on empirical evidence showing that larvae that contact the queen pupate earlier compared to larvae that are tended by only workers, and that the number of tending workers positively affects the final size of the developing larva. (a) Schematic graphical model for how changes in larval tending by the queen and workers throughout colony development can determine body size. Double dashed line: estimated percentage of brood care provided by the queen. Dotted line: number of workers nursing the brood. The blue diamonds (workers) and circles (gynes, top right of the plot), show the size of females emerging in a representative colony, and the linear regression model for the influence of colony age on body size (based on Shpigler *et al.* [52**]). (b) Summary of known interactions between the queen, the workers, and the developing larvae. Letters refers to the following references: a: Bloch *et al.* [65], b: Bortolotti *et al.* [66**], c: Pereboom *et al.* [67], d: Smeets and Duchateau [59], e: Boer and Duchateau [58**], f: Alaux *et al.* [68], g: Alaux *et al.* [69], h: Shpigler *et al.* [52**].

further diminish her influence on larval development relative to that of workers [64**]. The increase in number of brood tending bees further leads to an increase in final brood size, probably because more tending workers provide better care or more food to the developing larvae. Figure 3b summarizes additional evidence for social interactions affecting the development of *B. terrestris* larvae.

Endocrine and molecular mechanisms

Our understanding of the endocrine and molecular mechanisms determining body size in holometabolous insects is based mostly on experiments with model species, such as *M. sexta* and *D. melanogaster* [9,70,71]. These studies have identified the critical role of hormones such as Juvenile Hormone (JH), prothoracicotropic hormone (PTTH), and ecdysteroids, which together orchestrate the timing of metamorphosis, which in turn dictates larval mass at each molt. The mass of the last larval instar at which JH secretion ceases and its enzymatic breakdown is upregulated (termed the 'critical weight') is the most important processes determining the time of pupation and the size of the emerging adult [72]. Although there does not appear to be a critical weight in some solitary bees [38**], it is currently unknown whether this does exist in social bee species, and how this might operate in a system with highly variable worker sizes, such as bumble bees. At least part of the influence of

temperature on body size determination occurs via its regulation on the rate of enzymatic breakdown of JH. Body size increases with decreasing temperature because of a slow rate of JH clearance, which induces a longer development time and larger body size at pupation [12,73]. The insulin/insulin-like growth factor signaling (IIS) pathway is the key pathway linking nutrition to larval growth and is therefore also paramount for the regulation of larval growth and terminal size.

In solitary and some social bees, size variation is continuous, whereas in the eusocial bee species, queens and workers typically have non-overlapping size distributions. Caste determination, specifically in the highly social honey bees and stingless bees, provides some of the most remarkable evidence for polyphenism, the production of two or more distinct phenotypes from the same genome. In insect polyphenism, upstream environmental conditions are integrated by the brain, which in turn modulates patterns of secretion of developmental hormones such as JH, ecdysteroids, and IIS. The resultant endocrine signals direct alternative developmental trajectories that lead to the production of distinct phenotypes [74*]. These signaling pathways have been also implicated in the regulation of caste differentiation in the honey bee *A. mellifera*, the bee species in which the mechanisms underlying caste-differentiation are best studied [75,76]. Gyne-destined honey bee larvae are reared in special queen cells and are fed with

a distinctive royal jelly diet (see above Section ‘The control of larval diet by tending adults’). Subsequently, the insulin pathway mediates a diet-dependent elevation in the biosynthesis rate and circulating hemolymph titers of JH in queen-destined larvae. JH activates the expression of JH signaling genes such as *Kruppel-homolog 1 (Kr-h1)* and *Methoprene tolerance (Met)* to regulate downstream differential gene expression patterns underlying caste determination and differentiation [75–77]. JH may also affect gene expression by regulating epigenetic processes such as DNA methylation and expression of micro RNAs that have been implicated in caste determination [37,44–46]. Caste determination in the honey bee involves intricate processes other than those controlling body size, and these topics are beyond the scope of the current paper. JH and ecdysteroid titers are also higher in queen-destined versus worker-destined larvae, in the bumble bee *B. terrestris* [63,78,66**] (reviewed in Ref. [79]). Bortolotti *et al.* [66**] further reported that JH treatment affects larval growth and final body size in a dose-dependent and instar-dependent manner, with the higher doses applied to early instars resulting in development into gynes. Little is known about the molecular processes underlying caste differentiation in bumble bees, but as in honey bees, there is evidence for caste-specific expression of micro RNAs, suggesting their involvement in caste differentiation [80*]. Taken together, studies of insect metamorphosis, size determination, and caste differentiation in bees suggest that all of these processes are orchestrated by interplay between JH, ecdysteroids, and IIS. A major challenge for future research is to understand how the fine-scale temporal modulation of these same endocrine signaling pathways (and downstream molecular processes) regulates all these three pivotal processes.

Consequences of size variation in bees

Reproductive division of labor in social bees

Reproductive division of labor is a hallmark of insect societies, although the degree of reproductive skew and its relation to body size differs significantly among bee species with varying levels of social complexity. In most eusocial species, the exceedingly fertile queen is also larger than the less fertile workers [81,82]. Caste differentiation can also produce morphological or physiological variation that is beyond simple size variation (and thus beyond the scope of the current paper, see Section ‘Endocrine and molecular mechanisms’); these have been best explored in the honey bee *A. mellifera* [83], and to a lesser extent in stingless bees [84] and bumble bees [85].

In the relatively small and simple societies of some sweat bees and carpenter bees, there are no distinct female castes, but the first females to emerge can be smaller than later-emerging individuals, and only the latter will become the future reproductives [36,86,87]. In the sub-social and facultatively social small carpenter bee *Ceratina calcarata*, larger females are more likely to establish social

nests [88*]. The first daughter in social nests is typically smaller, non-reproductive, and behaves like a worker by helping to rear her sisters, who can potentially reproduce the following season (Figure 1a) [89]. Reproductive dominance is primarily determined via agonistic interactions in the less complex insect societies, where size commonly correlates with physical strength for winning aggressive contests. A good model for studies on dominance interactions is in foundresses associations, which have been best-studied in overwintered *Polistes* paper wasps [90–92], but are also found in several bees, such as carpenter bees (subfamily Xylocopini; e.g., *Xylocopa sulcatipes*, *Xylocopa pubescens*, *C. calcarata*), and sweat bees (family Halictidae; e.g., *Dialictus lineatulus*). Dominance hierarchies are also important in queenless bumble bee workers [93]. In these systems, larger females are more likely to reproduce and less likely to forage [40**,94,95].

Division of labor amongst workers in social species

Morphological polymorphism is pivotal to the organization of worker division of labor (known as ‘alloethism’) in many highly social species [81]. Although best studied in the morphologically distinct worker castes of ants and termites, recent studies report a similar morphologically specialized soldier subcaste in several genera of stingless bees (Figure 1c; Supplementary Table S1) [30**,54]. Other social bee species have overall morphologically similar workers that vary primarily in body size. Bumble bees follow this pattern, and show the most notable body size polymorphism among workers, with up to tenfold variability in mass in *Bombus terrestris* and *B. lucorum* [96] and ninefold in *B. impatiens* [97], (Figure 1b; Supplementary Table S1). Large bumble bee workers are more likely to forage, fan, and guard, than smaller bees, which typically perform in-nest activities such as brood tending [21,96,98–102]. Larger-bodied workers may also forage at an earlier age [98,99,102,103]. Even in colonies artificially composed of only medium size workers, and thus showing little size variability, foragers were still significantly larger than nurses, indicating that even small differences in size can affect the propensity to undertake certain tasks [Holland and Bloch, in revision]. There is evidence suggesting that even in honey bees, in which the division of labor relates to age [82], the little size variability among the workers still affects the age at which workers switch from in-nest to foraging activities [104]. New genomic studies in bumble bees are beginning to shed light on underlying drivers of the physiological and behavioral differences associated with worker size polymorphism. For example, there is evidence that small and large bees differ in the patterns of gene expression [105] and RNA editing [106].

Bees of certain body sizes may be better in performing some tasks, which can improve division of labor and overall colony performance. In bumble bees, large workers are more efficient in bringing pollen and nectar back to

the colony [21,22**,100], and also appear to have superior sensory capacities. They have more antennal sensilla and are better in detecting floral odors [107]. Their compound eyes are also larger, contain more ommatidia with a larger facet, and have improved visual discrimination [108]. Their ocelli are also larger, and they can fly under lower light intensities compared to smaller workers [109]. The larger eyes and ocelli may also contribute to their stronger phototactic response [110]. Large bumble bee workers are also better in some learning paradigms [97,111,112], have more circadian clock cells in their brains [113], and exhibit stronger circadian rhythms [102]. The latter may be important for sun-compass orientation and timing visits to flowers at their peak nectar production.

Size polymorphism as a strategy for optimal resource allocation

In spite of the evidence above suggesting that under some conditions small bees outperform larger ones, the primary value of smaller individuals may actually be the reduced cost of their production. The trade-off between offspring size and number is a common and well-studied life-history optimization strategy [4,5], and there is evidence that solitary bees can adjust the investment in offspring to optimize their fitness [39]. A bumble bee colony can theoretically substitute investment in a few highly capable large workers with a larger number of smaller, albeit less competent, individuals, whose greater numbers provide insurance against the loss of workers due to disease, predation, or other threats. Resource investment strategy is especially crucial during colony foundation, when the queen is alone, her resources are strictly limited, and wrong investment decisions can be fatal. If smaller workers are more resilient against starvation, as suggested by Couvillon and Dornhaus [25], then their production insures against the high resource unpredictability during colony foundation. This early-stage bet hedging strategy may help in achieving the later production of larger workers, males, and gynes. In addition, small individuals should take less time to develop and allow the queen to switch earlier to investment in egg-laying rather than brood provisioning [64**]. The evidence that in many annual species of bees the first brood of workers is composed of smaller individuals is consistent with this idea [20,32,40**,52**,88*].

Size polymorphism and pollination services

Body size may enable better exploitation of available floral resources. Both across [19] and within [109,114] bee species, body size is positively related to foraging range, and is also related to the capacity to carry greater amounts of pollen and nectar [22**]. Size can also affect the temporal niche of bees because it affects the temperatures in which bees can be active, and the size of the compound eyes can affect the minimal light intensity and time of day under which they can forage successfully [115*]. Some flowers are better handled by bees of a particular body size. For example, tongue length accounts

for some of the variation in flowers visited by large and small bumble bees, and impacts the efficiency of foraging in long versus short corolla flowers [11,116]. However, tongue lengths do not necessarily scale with overall body size within bee species [117]. The greater physical strength of large bees makes them better in handling some flowers. For example, in ‘tripping’, the insect’s legs and thorax expose the anthers and stigma of the flower [10]. In buzz pollination, bees hold a flower’s anthers and vibrate at a certain frequency in order to extract the pollen [118*], and here too, body size appears to be important in respect to amplitude [119*] or frequency [120*]. There is also evidence that some flowers are better handled by small bees [121]. In some stingless bees, such as *Melipona quadrifasciata* [20] and *M. flavolineata* [122], smaller foragers have larger corbiculae relative to their body size and are able to carry heavier loads of pollen per unit of body compared with larger individuals [20]. In social bees, size-variable individuals of the same species can pollinate a broader range of flower species within the same habitat [10,11,123], making them keystone pollinators in many pollination networks.

Summary and future directions

Body size variation is common in bees, and can be functionally significant for both solitary and social species. Given the sometimes conflicting and dynamic costs and benefits of body size, it is not surprising that body size is not always positively correlated with high fitness in bees [124–128]. As in other animals, it is assumed that the involvement of multiple factors on body size leads to stabilizing selection, where selective pressures and trade-offs favoring larger versus smaller sizes are balanced within populations [1]. In social bees such as bumble bees, body size polymorphism may be important for social organization because it influences two of the most important organization principles of insect societies: reproductive division of labor between queens and workers, and variation in task performance among workers. Thus, not surprisingly, in some social insects the regulation of body size is under strong social influence, in ways that we are only beginning to understand. In both solitary and social bees, there are significant maternal influences on brood development through control of diet composition, the brood cell, and the microenvironment (Figure 2), and also feeding rate in the progressively provisioning species. The situation is more complex in social bees, in which brood development is influenced by intricate interactions between the brood, the mother queen, and the workers. An important venue for future research is to understand how the different parties act to meet their interests, specifically in cases of conflict related to body size. To understand these complex systems, we will need to better understand communication between these interacting parties, including the chemical and functional characterization of hunger signals, and the ways in which tending adults respond to them. Much research is also needed to identify the specific nutrients or bioactive molecules that

play a role in size determination. Identification of these signals will allow us to understand how nutritional and social factors act on the molecular pathways that regulate larval development and ultimate body size. From a broader evolutionary perspective, comparative studies on these pathways across different bee lineages and across levels of social complexity will shed light on how body size evolves as a function of sociality, which is an overlooked aspect of the evolution of insect sociality.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.cois.2019.07.006>.

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- of special interest
- of outstanding interest

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