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Review

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Review

Ecological Drivers and Consequences of Bumble Bee Body Size Variation

Jacquelyn L. Fitzgerald,[1,2,3,4] **Jane E. Ogilvie,**[3] **and Paul J. CaraDonna**[1,2,3]

[1]Plant Biology and Conservation, Northwestern University, Evanston, IL 60201, USA, [2]Chicago Botanic Garden, Negaunee Institute for Plant Conservation Science & Action, Glencoe, IL 60022, USA, [3]Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA, and [4]Corresponding author, e-mail: jfitzgerald@chicagobotanic.org

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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. [Hymenoptera: Apidae]). 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.

Key words: bumble bee, *Bombus*, body size, size polymorphism

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) (Fig. 1). Within a single colony, *Bombus impatiens* Cresson (Hymenoptera: Apidae) 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, 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

Fig. 1. A) Size variation between a *B. flavifrons* Cresson queen (left), worker (center), and male (right); B) Size variation between *B. californicus* Smith queen (left) and worker (right); C) Size variation within *B. bifarius* Cresson workers. Specimens from the Rocky Mountain Biological Laboratory research collection.

(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 1955–2021 (Fig. 2A, Table 1, Supp Table 1 [online only]). 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* (Fig. 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* Linnaeus 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) (Fig. 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

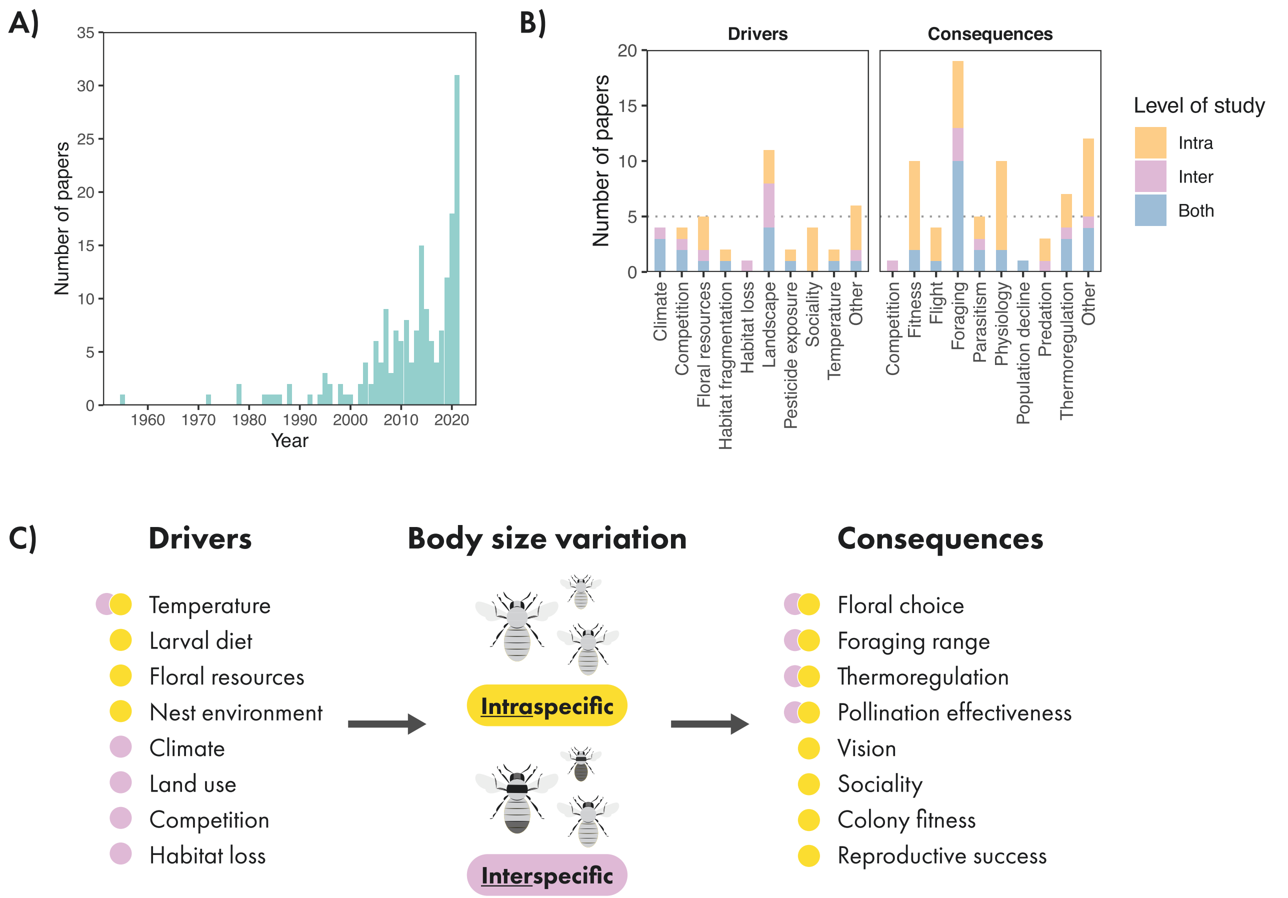

Fig. 2. (A) Number of papers on the drivers or consequences bumble bee body size across time. (B) Number of papers on the drivers and consequences of bumble bee body size divided by category and by the level of organization the paper considers: within species (*intraspecific*), between species (*interspecific*), or both. (C) Specific drivers and consequences of size variation within (*intraspecific*) and between species (*interspecific*).

(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_2 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) (Fig. 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 sonorous* Say (Williams et al. 2014) and the smaller, neotropical *B. pauloensis* Friese (Cameron and Jost 1998). Some species occur over broad climatic ranges, like the moderately-sized *B. griseocollis* De Geer, which can be found from the Southeastern USA to Northwestern Canada (Mitchell 1960), while others are more tightly constrained, like the large *B. polaris* Curtis and *B. alpines* Linnaeus, 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).

Table 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 Supp Table 1 [online only])

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

[a]Includes agriculture, urbanization, corridors, forest cover, wildfire.
[b]Includes foraging range, foraging rate, pollination effectiveness, floral choice.
[c]Includes vision, olfaction, circadian rhythms, immunocompetence.

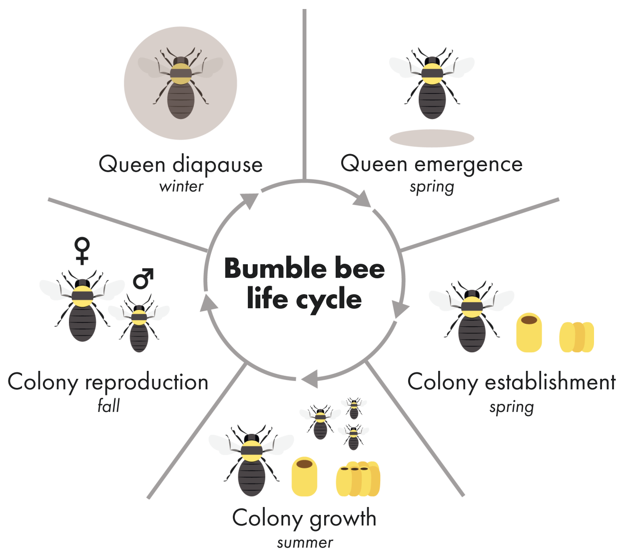

Fig. 3. Annual life cycle of a bumble bee colony. In the spring, bumble bee queens that were born the previous fall emerge from winter diapause and begin to forage. Queens that successfully found a nest will go on to produce a colony of workers. Towards the end of the growing season, the colony will produce sexual new queens and males. New queens will mate and enter diapause.

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 the number of native plant species appear to support 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* Radoszkowski (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 (Fig. 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 Meliffera Linnaeus [Hymenoptera: Apidae]) 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, 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, 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 et al. 2005a). 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 affects predator avoidance behavior. Across species, field evidence suggests 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. [Hymenoptera: Crabronidae]), sphecid wasps Sphecidae [Hymenoptera:Apoidea], 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 Brues [Diptera: Phoridae]), in addition to tracheal mites Locustacarus buchneri Stammer [Trombidiformes: Podapolipidae], intestinal parasites Crithidia bombi Léger [Trypanosomatida: Trypanosomatidae] and Vairimorpha bombi Fantham & Porter [Microsporidia: Nosematidae], and wax moths Aphomia sociella Linnaeus [Lepidoptera: Pyralidae], 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 opportunities to expose uninfected bees. If larger bees experience greater rates of parasitism, then this may further stress species and populations 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 (Fig. 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 (Fig. 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. 2020a), while some find 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 (Fig. 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 differ with the type of land use, i.e., exposure from conventional agricultural fields differs from that of urban yards. New generations pesticides, including noenicitinoids, 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

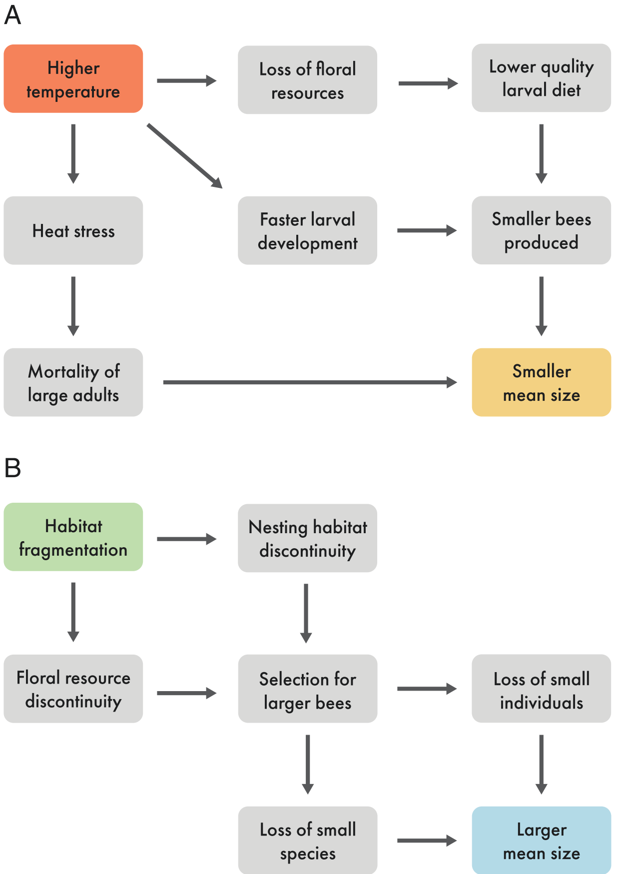

Fig. 4. (A) Hypothetical pathways by which higher temperatures could lead to smaller mean body size in bumble bees. Developmentally, higher temperatures could lead to smaller bees through the temperature-size rule or indirectly through changes in floral resources affecting larval nutrition. For adult 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.

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 an 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.

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Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

References Cited

Amin, M. R., L. Bussière, and D. Goulson. 2012. Effects of male age and size on mating success in the bumblebee *Bombus terrestris*. *J. Insect Behav*. 25: 362–374.

Arbetman, M. P., G. Gleiser, C. L. Morales, P. Williams, and M. A. Aizen. 2017. Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. *Proc. R. Soc. Lond. B Biol. Sci.* 284: 20170204.

Arroyo-Correa, B., C. Beattie, and M. Vallejo-Marín. 2019. Bee and floral traits affect the characteristics of the vibrations experienced by flowers during buzz pollination. *J. Exp. Biol.* 222: jeb198176.

Atkinson, D. 1996. Ectotherm life-history responses to developmental temperature, pp. 183–204. *In Animals and temperature: phenotypic and evolutionary adaptation*. Cambridge University Press.

Ayasse, M., T. Marlovits, J. Tengö, T. Taghizadeh, and W. Francke. 1995. Are there pheromonal dominance signals in the bumblebee *Bombus hypnorum L* (Hymenoptera, Apidae)? *Apidologie*. 26: 163–180.

Baeuerle, G., H. Feldhaar, and O. Otti. 2020. Comparing a potential external immune defense trait to internal immunity in females of wild bumblebees. *Front. Ecol. Evol.* 8: 62.

Balfour, N. J., K. Shackleton, N. A. Arscott, K. Roll-Baldwin, A. Bracuti, G. Toselli, and F. L. Ratnieks. 2021. Energetic efficiency of foraging mediates bee niche partitioning. *Ecology*. 102: e03285.

Barrow, D., and R. Pickard. 1984. Size-related selection of food plants by bumblebees. *Ecol. Entomol.* 9: 369–373.

Bartomeus, I., J. S. Ascher, J. Gibbs, B. N. Danforth, D. L. Wagner, S. M. Hedtke, and R. Winfree. 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proc. Natl. Acad. Sci. U. S. A.* 110: 4656–4660.

Bennett, A. B., and S. Lovell. 2019. Landscape and local site variables differentially influence pollinators and pollination services in urban agricultural sites. *PLoS One*. 14: e0212034.

Bergmann, C. 1848. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.

Bernauer, O. M., H. R. Gaines-Day, and S. A. Steffan. 2015. Colonies of bumble bees (*Bombus impatiens*) produce fewer workers, less bee biomass, and have smaller mother queens following fungicide exposure. *Insects*. 6: 478–488.

Biella, P. 2015. *Bombus (Alpinobombus) alpinus* in the Italian Central Alps (Hymenoptera: Apidae: Bombinae). *Il. Nat. Valtellin*. 25: 69–72.

Bishop, J., and W. Armbruster. 1999. Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny and ecology. *Funct. Ecol*. 13: 711–724.

Blacquiere, T., G. Smagghe, C. A. Van Gestel, and V. Mommaerts. 2012. Neonicotinoids in bees: a review on concentrations, side-effects and risk assessment. *Ecotoxicology*. 21: 973–992.

Bourke, A. F. 1997. Sex ratios in bumble bees. *Philos. Trans. R. Soc. Lond. Ser. B*. 352: 1921–1933.

Bowers, M. A. 1985. Experimental analyses of competition between two species of bumble bees (Hymenoptera: Apidae). *Oecologia*. 67: 224–230.

Brand, N., and M. Chapuisat. 2012. Born to be bee, fed to be worker? The caste system of a primitively eusocial insect. *Front. Zool*. 9: 351–359.

Burdine, J. D., and K. E. McCluney. 2019. Interactive effects of urbanization and local habitat characteristics influence bee communities and flower visitation rates. *Oecologia*. 190: 715–723.

Calder, W. A. 1996. *Size, function, and life history*. Harvard University Press, Cambridge, MA: Courier Corporation.

Cameron, S., and M. Jost. 1998. Mediators of dominance and reproductive success among queens in the cyclically polygynous Neotropical bumble bee *Bombus atratus Franklin*. *Insectes Soc*. 45: 135–149.

Cameron, S. A., and B. M. Sadd. 2020. Global trends in bumble bee health. *Annu. Rev. Entomol*. 65: 209–232.

Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proc. Natl. Acad. Sci. U. S. A*. 108: 662–667.

CaraDonna, P. J., and N. M. Waser. 2020. Temporal flexibility in the structure of plant–pollinator interaction networks. *Oikos*. 129: 1369–1380.

CaraDonna, P. J., J. L. Cunningham, and A. M. Iler. 2018. Experimental warming in the field delays phenology and reduces body mass, fat content and survival: implications for the persistence of a pollinator under climate change. *Funct. Ecol*. 32: 2345–2356.

Cariveau, D. P., G. K. Nayak, I. Bartomeus, J. Zientek, J. S. Ascher, J. Gibbs, and R. Winfree. 2016. The allometry of bee proboscis length and its uses in ecology. *PLoS One*. 11: e0151482.

Cartar, R. V. 1992. Adjustment of foraging effort and task switching in energy-manipulated wild bumblebee colonies. *Anim. Behav*. 44: 75–87.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst*. 31: 343–366.

Chole, H., S. H. Woodard, and G. Bloch. 2019. Body size variation in bees: regulation, mechanisms, and relationship to social organization. *Curr. Opin. Insect Sci*. 35: 77–87.

Cnaani, J., and A. Hefetz. 1994. The effect of workers size frequency distribution on colony development in *Bombus terrestris*. *Insectes Soc*. 41: 301–307.

Cohen, H., G. P. Smith, H. Sardiñas, J. F. Zorn, Q. S. McFrederick, S. H. Woodard, and L. C. Ponisio. 2021. Mass-flowering monoculture attracts bees, amplifying parasite prevalence. *Proc. R. Soc. B*. 288: 20211369.

Colla, S. R., M. C. Otterstatter, R. J. Gegear, and J. D. Thomson. 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biol. Conserv*. 129: 461–467.

Costa, C. P., K. Fisher, B. M. Guillén, N. Yamanaka, G. Bloch, and S. H. Woodard. 2021. Care-giver identity impacts offspring development and performance in an annually social bumble bee. *BMC Ecol. Evol*. 21: 1–11.

Couvillon, M. J., and A. Dornhaus. 2009. Location, location, location: larvae position inside the nest is correlated with adult body size in worker bumblebees (*Bombus impatiens*). *Proc. R. Soc. B Biol. Sci*. 276: 2411–2418.

Couvillon, M. J., and A. Dornhaus. 2010. Small worker bumble bees (Bombus impatiens) are hardier against starvation than their larger sisters. *Insectes Soc*. 57: 193–197.

Couvillon, M. J., G. Fitzpatrick, and A. Dornhaus. 2010a. Ambient air temperature does not predict whether small or large workers forage in bumble bees (*Bombus impatiens*). *Psyche*. 1–8.

Couvillon, M. J., J. M. Jandt, N. Duong, and A. Dornhaus. 2010b. Ontogeny of worker body size distribution in bumble bee (*Bombus impatiens*) colonies. *Ecol. Entomol*. 35: 424–435.

Couvillon, M. J., J. M. Jandt, J. Bonds, B. R. Helm, and A. Dornhaus. 2011. Percent lipid is associated with body size but not task in the bumble bee *Bombus impatiens*. *J. Comp. Physiol. A*. 197: 1097–1104.

Crall, J. D., N. Gravish, A. M. Mountcastle, S. D. Kocher, R. L. Oppenheimer, N. E. Pierce, and S. A. Combes. 2018. Spatial fidelity of workers predicts collective response to disturbance in a social insect. *Nat. Commun*. 9: 1–13.

Cueva del Castillo, R., S. Sanabria-Urbán, and A. M. Serrano-Meneses. 2015. Trade-offs in the evolution of bumblebee colony and body size: a comparative analysis. *Ecol. Evol*. 5: 3926–3914.

De Luca, P. A., D. A. Cox, and M. Vallejo-Marín. 2014. Comparison of pollination and defensive buzzes in bumblebees indicates species-specific and context-dependent vibrations. *Naturwissenschaften*. 101: 331–338.

De Luca, P. A., S. Buchmann, C. Galen, A. C. Mason, and M. Vallejo-Marín. 2019. Does body size predict the buzz-pollination frequencies used by bees? *Ecol. Evol*. 9: 4875–4887.

De Palma, A., M. Kuhlmann, S. P. Roberts, S. G. Potts, L. Börger, L. N. Hudson, I. Lysenko, T. Newbold, and A. Purvis. 2015. Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. *J. Appl. Ecol*. 52: 1567–1577.

Dukas, R., and D. H. Morse. 2003. Crab spiders affect flower visitation by bees. *Oikos*. 101: 157–163.

Durrer, S., and P. Schmid-Hempel. 1995. Parasites and the regional distribution of bumblebee species. *Ecography*. 18: 114–122.

Edens-Meier, R., M. Arduser, E. Westhus, and P. Bernhardt. 2011. Pollination ecology of *Cypripedium reginae* Walter (Orchidaceae): size matters. *Telopea*. 13: 327–340.

Eggenberger, H., D. Frey, L. Pellissier, J. Ghazoul, S. Fontana, and M. Moretti. 2019. Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *J. Anim. Ecol*. 88: 1522–1533.

Elbgami, T., W. E. Kunin, W. O. Hughes, and J. C. Biesmeijer. 2014. The effect of proximity to a honeybee apiary on bumblebee colony fitness, development, and performance. *Apidologie*. 45: 504–513.

Evans, L. J., and N. E. Raine. 2014. Changes in learning and foraging behaviour within developing bumble bee (*Bombus terrestris*) colonies. *PLoS One*. 9: e90556.

Figueroa, L. L., S. Compton, H. Grab, and S. H. McArt. 2021. Functional traits linked to pathogen prevalence in wild bee communities. *Sci. Rep*. 11: 1–12.

Fletcher, D. J., and K. G. Ross. 1985. Regulation of reproduction in eusocial Hymenoptera. *Annu. Rev. Entomol*. 30: 319–343.

Földesi, R., B. G. Howlett, I. Grass, and P. Batáry. 2021. Larger pollinators deposit more pollen on stigmas across multiple plant species—a meta-analysis. *J. Appl. Ecol*. 58: 699–707.

Forrest, J. R. 2015. Plant–pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? *Oikos*. 124: 4–13.

Foster, D. J., and R. V. Cartar. 2011. Wing wear affects wing use and choice of floral density in foraging bumble bees. *Behav. Ecol*. 22: 52–59.

Foster, R. L., A. Brunskill, D. Verdirame, and S. O'Donnell. 2004. Reproductive physiology, dominance interactions, and division of labour among bumble bee workers. *Physiol. Entomol*. 29: 327–334.

Free, J. B. 1955a. The division of labour within bumblebee colonies. *Insectes Soc*. 2: 195–212.

Free, J. B. 1955b. The collection of food by bumblebees. *Insectes Soc*. 2: 303–311.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming?. *Trends Ecol. Evol*. 26: 285–291.

Gavini, S. S., C. Quintero, and M. Tadey. 2020. Intraspecific variation in body size of bumblebee workers influences anti-predator behaviour. *J. Anim. Ecol*. 89: 658–669.

Gayer, C., A. Biermann, M. Dieterich, K. Reidl, and P. Batáry. 2021. Organic winter cereals benefit bumblebee colonies in agricultural landscapes with mass-flowering crops. *Insect Conserv. Diver*. 14: 504–514.

Gérard, M., M. Vanderplanck, M. Franzen, M. Kuhlmann, S. G. Potts, P. Rasmont, O. Schweiger, and D. Michez. 2018. Patterns of size variation in bees at a continental scale: does Bergmann's rule apply? *Oikos*. 127: 1095–1103.

Gérard, M., B. Martinet, K. Maebe, L. Marshall, G. Smagghe, N. J. Vereecken, S. Vray, P. Rasmont, and D. Michez. 2020. Shift in size of bumblebee queens over the last century. *Glob. Change Biol*. 26: 1185–1195.

Gérard, M., L. Marshall, B. Martinet, and D. Michez. 2021. Impact of landscape fragmentation and climate change on body size variation of bumblebees during the last century. *Ecography*. 44: 255–264.

Gillespie, S. D., K. Carrero, and L. S. Adler. 2015. Relationships between parasitism, bumblebee foraging behaviour, and pollination service to *Trifolium pratense* flowers. *Ecol. Entomol*. 40: 650–653.

Goulson, D. 2003. *Bumblebees: their behaviour and ecology*. Oxford University Press, USA.

Goulson, D. 2010. *Bumblebees: behaviour, ecology, and conservation*. Oxford University Press on Demand.

Goulson, D., and K. R. Sparrow. 2009. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *J. Insect Conserv*. 13: 177–181.

Goulson, D., J. Peat, J. C. Stout, J. Tucker, B. Darvill, L. C. Derwent, and W. O. Hughes. 2002. Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency? *Anim. Behav*. 64: 123–130.

Grass, I., J. Albrecht, N. Farwig, and F. Jauker. 2021. Plant traits and landscape simplification drive intraspecific trait diversity of *Bombus terrestris* in wildflower plantings. *Basic Appl. Ecol*. 57: 91–101.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia*. 153: 589–596.

Guiraud, M., B. Cariou, M. Henrion, E. Baird, and M. Gérard. 2021. Higher developmental temperature increases queen production and decreases worker body size in the bumblebee Bombus terrestris. *J. Hymenopt. Res*. 88: 39–49.

Hagen, M., and Y. L. Dupont. 2013. Inter-tegular span and head width as estimators of fresh and dry body mass in bumblebees (Bombus spp.). *Insectes Soc*. 60: 251–257.

Hall, K., T. Robert, K. J. Gaston, and N. Hempel de Ibarra. 2021. Onset of morning activity in bumblebee foragers under natural low light conditions. *Ecol. Evol*. 11: 6536–6545.

Hamblin, A. L., E. Youngsteadt, M. M. Lopez-Uribe, and S. D. Frank. 2017. Physiological thermal limits predict differential responses of bees to urban heat-island effects. *Biol. Lett*. 13: 20170125.

Harder, L. D. 1986. Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. *Oecologia*. 69: 309–315.

Heinrich, B. 2004. *Bumblebee economics*. Cambridge, MA: Harvard University Press.

Heinrich, B. H., and J. E. Margaret. 1983. Size and caste in temperature regulation by bumblebees. *Physiol. Zool*. 56: 552–562.

Hendriksma, H. P., A. L. Toth, and S. Shafir. 2019. Individual and colony level foraging decisions of bumble bees and honey bees in relation to balancing of nutrient needs. *Front. Ecolo. Evol*. 7: 177.

Herrmann, J. D., N. M. Haddad, and D. J. Levey. 2018. Mean body size predicts colony performance in the common eastern bumble bee (*Bombus impatiens*). *Ecol. Entomol*. 43: 458–462.

Hirsch, M., S. Pfaff, and V. Wolters. 2003. The influence of matrix type on flower visitors of *Centaurea jacea* L. *Agric. Ecosyst. Environ*. 98: 331–337.

Holland, J. G., S. Nakayama, M. Porfiri, O. Nov, and G. Bloch. 2021. Body size and behavioural plasticity interact to influence the performance of free-foraging bumble bee colonies. *Insects*. 12: 236.

Holm, S. N. 1972. Weight and life length of hibernating bumble bee queens (Hymenoptera: Bombidae) under controlled conditions. *Insect Syst. Evol*. 3: 313–320.

Hung, K. J., S. S. Sandoval, J. S. Ascher, and D. A. Holway. 2021. Joint impacts of drought and habitat fragmentation on native bee assemblages in a California biodiversity hotspot. *Insects*. 12: 135.

Hutchinson, L. A., T. H. Oliver, T. D. Breeze, R. S. O'Connor, S. G. Potts, S. P. Roberts, and M. P. Garratt. 2021. Inventorying and monitoring crop pollinating bees: evaluating the effectiveness of common sampling methods. *Insect Conserv. Diver*. 15: 299–311.

Ings, T. C. 2005. Body size affects nectar uptake rates in bumblebees (Hymenoptera: Apidae: *Bombus terrestris*). *Entomol. Gen*. 30: 186–186.

Ings, T. C., J. Schikora, and L. Chittka. 2005. Bumblebees, humble pollinators or assiduous invaders? A population comparison of foraging performance in *Bombus terrestris*. *Oecologia*. 144: 508–516.

Ings, T., N. Ward, and L. Chittka. 2006. Can commercially imported bumble bees out-compete their native conspecifics? *J. Appl. Ecol*. 43: 940–948.

Inoue, M. N. 2011. Size-dependent selection against small queens of the invasive bumblebee *Bombus terrestris* in Japan. *Entomol. Exp. Appl*. 138: 65–70.

Inoue, M. N., and J. Yokoyama. 2006. Morphological variation in relation to flower use in bumblebees. *Entomol. Sci*. 9: 147–159.

Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. *Ecology*. 59: 672–678.

Jandt, J. M., and A. Dornhaus. 2014. Bumblebee response thresholds and body size: does worker diversity increase colony performance? *Anim. Behav*. 87: 97–106.

Jandt, J. M., E. Huang, and A. Dornhaus. 2009. Weak specialization of workers inside a bumble bee (*Bombus impatiens*) nest. *Behav. Ecol. Sociobiol*. 63: 1829–1836.

Jandt, J. M., S. Suryanarayanan, J. C. Hermanson, R. L. Jeanne, and A. L. Toth. 2017. Maternal and nourishment factors interact to influence offspring developmental trajectories in social wasps. *Proc. R. Soc. B Biol. Sci*. 284: 20170651.

Jauker, B., J. Krauss, F. Jauker, and I. Steffan-Dewenter. 2012. Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landsc. Ecol*. 28: 107–120.

Jones, E. I., and A. Dornhaus. 2011. Predation risk makes bees reject rewarding flowers and reduce foraging activity. *Behav. Ecol. Sociobiol*. 65: 1505–1511.

Kapustjanskij, A., M. Streinzer, H. Paulus, and J. Spaethe. 2007. Bigger is better: implications of body size for flight ability under different light conditions and the evolution of alloethism in bumblebees. *Funct. Ecol*. 21: 1130–1136.

Kelber, A., and H. Somanathan. 2019. Spatial vision and visually guided behavior in Apidae. *Insects*. 10: 418.

Kelemen, E., and A. Dornhaus. 2018. Lower temperatures decrease worker size variation but do not affect fine-grained thermoregulation in bumble bees. *Behav. Ecol. Sociobiol*. 72: 170.

Kelemen, E. P., N. Cao, T. Cao, G. Davidowitz, and A. Dornhaus. 2019. Metabolic rate predicts the lifespan of workers in the bumble bee *Bombus impatiens*. *Apidologie*. 50: 195–203.

Kelemen, E. P., G. Davidowitz, and A. Dornhaus. 2020. Size variation does not act as insurance in bumble bees; instead, workers add weight in an unpredictable environment. *Anim. Behav*. 170: 99–109.

Kenna, D., S. Pawar, and R. J. Gill. 2021. Thermal flight performance reveals impact of warming on bumblebee foraging potential. *Funct. Ecol*. 35: 2508–2522.

Kerr, N. Z., E. E. Crone, and N. M. Williams. 2019. Integrating vital rates explains optimal worker size for resource return by bumblebee workers. *Funct. Ecol*. 33: 467–478.

Kerr, N. Z., R. L. Malfi, N. M. Williams, and E. E. Crone. 2021. Larger workers outperform smaller workers across resource environments: an evaluation of demographic data using functional linear models. *Ecol. Evol*. 11: 2814–2827.

Kingsolver, J. G., and R. B. Huey. 2008. Size, temperature, and fitness: three rules. *Evol. Ecol. Res*. 10: 251–268.

Klein, S., C. Pasquaretta, A. B. Barron, J. -M. Devaud, and M. Lihoreau. 2017. Inter-individual variability in the foraging behaviour of traplining bumblebees. *Sci. Rep*. 7: 1–12.

Knee, W., and J. Medler. 1965. The seasonal size increase of bumblebee workers (Hymenoptera: *Bombus*). *Can. Entomol*. 97: 1149–1155.

Koski, M. H., J. L. Ison, A. Padilla, A. Q. Pham, and L. F. Galloway. 2018. Linking pollinator efficiency to patterns of pollen limitation: small bees exploit the plant–pollinator mutualism. *Proc. R. Soc. B Biol. Sci*. 285: 20180635.

Kuppler, J., J. Wieland, R. R. Junker, and M. Ayasse. 2021. Drought-induced reduction in flower size and abundance correlates with reduced flower visits by bumble bees. *AoB Plants*. 13: plab001.

Kuris, A. M., A. R. Blaustein, and J. J. Alio. 1980. Hosts as islands. *Am. Nat*. 116: 570–586.

Kuriya, S., M. Hattori, Y. Nagano, and T. Itino. 2015. Altitudinal flower size variation correlates with local pollinator size in a bumblebee-pollinated herb, *Prunella vulgaris* L. (Lamiaceae). *J. Evol. Biol*. 28: 1761–1769.

Leiva, F. P., P. Calosi, and W. C. Verberk. 2019. Scaling of thermal tolerance with body mass and genome size in ectotherms: a comparison between water-and air-breathers. *Philos. Trans. R. Soc. B*. 374: 20190035.

Liang, H., Y. H. Zhao, N. E. Rafferty, Z. X. Ren, L. Zhong, H. D. Li, D. Z. Li, and H. Wang. 2021. Evolutionary and ecological factors structure a plant–bumblebee network in a biodiversity hotspot, the Himalaya–Hengduan Mountains. *Funct. Ecol*. 35: 2523–2535.

Maas, B., M. Brandl, R. I. Hussain, T. Frank, K. P. Zulka, D. Rabl, R. Walcher, and D. Moser. 2021. Functional traits driving pollinator and predator responses to newly established grassland strips in agricultural landscapes. *J. Appl. Ecol*. 58: 1728–1737.

Maebe, K., I. Meeus, and G. Smagghe. 2013. Recruitment to forage of bumblebees in artificial low light is less impaired in light sensitive colonies, and not only determined by external morphological parameters. *J. Insect Physiol*. 59: 913–918.

Maebe, K., A. De Baets, P. Vandamme, N. J. Vereecken, D. Michez, and G. Smagghe. 2021. Impact of intraspecific variation on measurements of thermal tolerance in bumble bees. *J. Therm. Biol*. 99: 103002.

Malfi, R. L., and T. a. H. Roulston. 2014. Patterns of parasite infection in bumble bees (*Bombus* spp.) of Northern Virginia. *Ecol. Entomol*. 39: 17–29.

Malfi, R. L., E. Crone, and N. Williams. 2019. Demographic benefits of early season resources for bumble bee (*B. vosnesenskii*) colonies. *Oecologia*. 191: 377–388.

Martinet, B., S. Dellicour, G. Ghisbain, K. Przybyla, E. Zambra, T. Lecocq, M. Boustani, R. Baghirov, D. Michez, and P. Rasmont. 2020. Global effects of extreme temperatures on wild bumblebees. *Conserv. Biol*. 35: 1507–1518.

Medler, J. T. 1962. Morphometric studies on bumble bees. *Ann. Entomol. Soc. Am*. 55: 212–218.

Merling, M., S. Eisenmann, and G. Bloch. 2020. Body size but not age influences phototaxis in bumble bee (*Bombus terrestris*, L.) workers. *Apidologie*. 51: 763–776.

Michener, C. D. 2000. *The bees of the world*, vol. 1. Baltimore, MD: Johns Hopkins University Press.

Miller-Struttmann, N. E., D. Heise, J. Schul, J. C. Geib, and C. Galen. 2017. Flight of the bumble bee: buzzes predict pollination services. *PLoS One*. 12: e0179273.

Mitchell, T. B. 1960. Bees of the eastern United States.

Mola, J. M., M. R. Miller, S. M. O'Rourke, and N. M. Williams. 2020. Forests do not limit bumble bee foraging movements in a montane meadow complex. *Ecol. Entomol*. 45: 955–965.

Morales, C. L., M. P. Arbetman, S. A. Cameron, and M. A. Aizen. 2013. Rapid ecological replacement of a native bumble bee by invasive species. *Front. Ecol. Environ*. 11: 529–534.

Morandin, L. A., M. L. Winston, M. T. Franklin, and V. A. Abbott. 2005. Lethal and sub-lethal effects of spinosad on bumble bees (*Bombus impatiens* Cresson). *Pest Manag. Sci*. 61: 619–626.

Morse, D. H. 1978. Size-related foraging differences of bumble bee workers. *Ecol. Entomol*. 3: 189–192.

Muller, C., and P. Schmid-Hempel. 1992. Variation in life-history pattern in relation to worker mortality in the bumble-bee, *Bombus lucorum*. *Funct. Ecol*. 6: 48–56.

Muller, C. B., T. M. Blackburn, and P. Schmid-Hempel. 1996. Field evidence that host selection by conopid parasitoids is related to host body size. *Insectes Soc*. 43: 227–233.

Murúa, M. M., A. A. Grez, and J. A. Simonetti. 2011. Changes in wing length in the pollinator *Bombus dahlbomii* occurring with the fragmentation of the Maulino forest, Chile. *Cienc. Investig. Agrar*. 38: 391–396.

Nagamitsu, T., T. Kenta, N. Inari, E. Kato, and T. Hiura. 2006. Abundance, body size, and morphology of bumblebees in an area where an exotic species, *Bombus terrestris*, has colonized in Japan. *Ecol. Res*. 22: 331–341.

Nagamitsu, T., H. Yamagishi, T. Kenta, N. Inari, and E. Kato. 2010. Competitive effects of the exotic *Bombus terrestris* on native bumble bees revealed by a field removal experiment. *Popul. Ecol*. 52: 123–136.

Nooten, S. S., and S. M. Rehan. 2020. Historical changes in bumble bee body size and range shift of declining species. *Biodivers. Conserv*. 29: 451–467.

Ohashi, K., A. Leslie, and J. D. Thomson. 2008. Trapline foraging by bumble bees: V. Effects of experience and priority on competitive performance. *Behav. Ecol*. 19: 936–948.

Oliveira, M. O., B. M. Freitas, J. Scheper, and D. Kleijn. 2016. Size and sex-dependent shrinkage of Dutch bees during one-and-a-half centuries of land-use change. *PLoS One*. 11: e0148983.

Osorio-Canadas, S., X. Arnan, A. Rodrigo, A. Torne-Noguera, R. Molowny, and J. Bosch. 2016. Body size phenology in a regional bee fauna: a temporal extension of Bergmann's rule. *Ecol. Lett*. 19: 1395–1402.

Otterstatter, M. C. 2004. Patterns of parasitism among conopid flies parasitizing bumblebees. *Entomol. Exp. Appl*. 111: 133–139.

Otti, O., and P. Schmid-Hempel. 2007. Nosema bombi: a pollinator parasite with detrimental fitness effects. *J. Invertebr. Pathol*. 96: 118–124.

Owen, R. E. 1988. Body size variation and optimal body size of bumble bee queens (Hymenoptera: Apidae). *Can. Entomol*. 120: 19–27.

Oyen, K. J., and M. E. Dillon. 2018. Critical thermal limits of bumblebees (*Bombus impatiens*) are marked by stereotypical behaviors and are unchanged by acclimation, age or feeding status. *J. Exp. Biol*. 221: jeb165589.

Oyen, K. J., S. Giri, and M. E. Dillon. 2016. Altitudinal variation in bumble bee (Bombus) critical thermal limits. *J. Therm. Biol*. 59: 52–57.

Oyen, K. J., L. E. Jardine, Z. M. Parsons, J. D. Herndon, J. P. Strange, J. D. Lozier, and M. E. Dillon. 2021. Body mass and sex, not local climate, drive differences in chill coma recovery times in common garden reared bumble bees. *J. Comp. Physiol. B*. 191: 843–854.

Pachauri, R. K., M. R. Allen, V. R. Barros, J. Broome, W. Cramer, R. Christ, J. A. Church, L. Clarke, Q. Dahe, and P. Dasgupta. 2014. Climate change 2014: synthesis report. *In* Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change, IPCC.

Pandey, A., U. Motro, and G. Bloch. 2020. Juvenile hormone interacts with multiple factors to modulate aggression and dominance in groups of orphan bumble bee (*Bombus terrestris*) workers. *Horm. Behav*. 117: 104602.

Peat, J., J. Tucker, and D. Goulson. 2005a. Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers? *Ecol. Entomol*. 30: 176–181.

Peat, J., B. Darvill, J. Ellis, and D. Goulson. 2005b. Effects of climate on intra- and interspecific size variation in bumble-bees. *Funct. Ecol*. 19: 145–151.

Pelletier, L., and J. N. McNeil. 2003. The effect of food supplementation on reproductive success in bumblebee field colonies. *Oikos*. 103: 688–694.

Pendrel, B., and R. Plowright. 1981. Larval feeding by adult bumble bee workers (Hymenoptera: Apidae). *Behav. Ecol. Sociobiol*. 8: 71–76.

Persson, A. S., and H. G. Smith. 2011. Bumblebee colonies produce larger foragers in complex landscapes. *Basic Appl. Ecol*. 12: 695–702.

Peters, R. H., and R. H. Peters. 1986. *The ecological implications of body size*, vol. 2. Cambridge , UK: Cambridge University Press.

Plowright, R., J. D. Thomson, L. Lefkovitch, and C. Plowright. 1993. An experimental study of the effect of colony resource level manipulation on foraging for pollen by worker bumble bees (Hymenoptera: Apidae). *Can. J. Zool*. 71: 1393–1396.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol*. 25: 345–353.

Princen, S. A., A. Van Oystaeyen, J. S. van Zweden, and T. Wenseleers. 2020. Worker dominance and reproduction in the bumblebee *Bombus terrestris*: when does it pay to bare one's mandibles? *Anim. Behav*. 166: 41–50.

Pyke, G. H. 1978. Optimal body size in bumblebees. *Oecologia*. 34: 255–266.

Pyke, G. H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecology*. 63: 555–573.

Raine, N. E., and L. Chittka. 2005. Comparison of flower constancy and foraging performance in three bumblebee species (Hymenoptera: Apidae: *Bombus*). *Entomol. Gen*. 28: 81081–81089.

Raine, N. E., and L. Chittka. 2008. The correlation of learning speed and natural foraging success in bumble-bees. *Proc. R. Soc. B Biol. Sci*. 275: 803–808.

Ramírez-Delgado, V. H., S. Sanabria-Urbán, M. A. Serrano-Meneses, and R. Cueva del Castillo. 2016. The converse to Bergmann's rule in bumblebees, a phylogenetic approach. *Ecol. Evol*. 6: 6160–6169.

Ranta, E. 1984. Proboscis length and the coexistence of bumblebee species. *Oikos*. 43: 189–196.

Ranta, E., and K. Vepsäläinen. 1981. Why are there so many species? Spatio-temporal heterogeneity and northern bumblebee communities. *Oikos*. 36: 28–34.

Ranta, E., and M. Tiainen. 1982. Structure in seven bumblebee communities in eastern Finland in relation to resource availability. *Ecography*. 5: 48–54.
Riveros, A. J., and W. Gronenberg. 2009. Olfactory learning and memory in the bumblebee Bombus occidentalis. *Naturwissenschaften*. 96: 851–856.
Robinson, G. E. 1992. Regulation of division of labor in insect societies. *Annu. Rev. Entomol*. 37: 637–665.
Rosi-Denadai, C. A., P. C. S. Araújo, L. A. d. O. Campos, L. Cosme Jr, and R. N. C. Guedes. 2020. Buzz-pollination in Neotropical bees: genus-dependent frequencies and lack of optimal frequency for pollen release. *Insect Sci*. 27: 133–142.
Rotheray, E. L., J. L. Osborne, and D. Goulson. 2017. Quantifying the food requirements and effects of food stress on bumble bee colony development. *J. Apic. Res*. 56: 288–299.
Roulston, T. a. H., and J. H. Cane. 2002. The effect of pollen protein concentration on body size in the sweat bee *Lasioglossum zephyrum* (Hymenoptera: Apiformes). *Evol. Ecol*. 16: 49–65.
Roulston, T. a. C., and H. James. 2000. The effect of diet breadth and nesting ecology of body size variation in bees. *J. Kans. Entomol. Soc*. 73: 129–142.
Russell, A. L., A. M. Fetters, E. I. James, and T.-L. Ashman. 2021. Pollinator effectiveness is affected by intraindividual behavioral variation. *Oecologia*. 197: 189–200.
Schmid-Hempel, R., and P. Schmid-Hempel. 1996. Host choice and fitness correlates for conopid flies parasitising bumblebees. *Oecologia*. 107: 71–78.
Schmid-Hempel, R., and P. Schmid-Hempel. 1998. Colony performance and immunocompetence of a social insect, *Bombus terrestris*, in poor and variable environments. *Funct. Ecol*. 12: 22–30.
Scriven, J. J., P. R. Whitehorn, D. Goulson, and M. C. Tinsley. 2016. Bergmann's body size rule operates in facultatively endothermic insects: evidence from a complex of cryptic Bumblebee species. *PLoS One*. 11: e0163307.
Sheridan, J. A., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. *Nat. Clim. Change*. 1: 401–406.
Shpigler, H., M. Tamarkin, Y. Gruber, M. Poleg, A. J. Siegel, and G. Bloch. 2013. Social influences on body size and developmental time in the bumblebee *Bombus terrestris*. *Behav. Ecol. Sociobiol*. 67: 1601–1612.
Simanonok, M. P., and L. A. Burkle. 2014. Partitioning interaction turnover among alpine pollination networks: spatial, temporal, and environmental patterns. *Ecosphere*. 5: art1491–aart149.
Siviter, H., S. K. Richman, and F. Muth. 2021. Field-realistic neonicotinoid exposure has sub-lethal effects on non-Apis bees: a meta-analysis. *Ecol. Lett*. 24: 2586–2597.
Sladen, F. W. L. 1912. *The humble-bee*. Cambridge, UK: Cambridge University Press.
Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *Am. Nat*. 108: 499–506.
Soroye, P., T. Newbold, and J. Kerr. 2020. Climate change contributes to widespread declines among bumble bees across continents. *Science*. 367: 685–688.
Spaethe, J., and L. Chittka. 2003. Interindividual variation of eye optics and single object resolution in bumblebees. *J. Exp. Biol*. 206: 3447–3453.
Spaethe, J., and A. Weidenmüller. 2002. Size variation and foraging rate in bumblebees (Bombus terrestris). *Insectes Soc*. 49: 142–146.
Spaethe, J., A. Brockmann, C. Halbig, and J. Tautz. 2007. Size determines antennal sensitivity and behavioral threshold to odors in bumblebee workers. *Naturwissenschaften*. 94: 733–739.
Stone, G., and P. Willmer. 1989. Warm-up rates and body temperatures in bees: the importance of body size, thermal regime and phylogeny. *J. Exp. Biol*. 147: 303–328.
Stout, J. C. 2000. Does size matter? Bumblebee behaviour and the pollination of *Cytisus scoparius* L. (Fabaceae). *Apidologie*. 31: 129–139.
Straw, E. A., and M. J. Brown. 2021. Co-formulant in a commercial fungicide product causes lethal and sub-lethal effects in bumble bees. *Sci. Rep*. 11: 1–10.
Straw, E. A., E. N. Carpentier, and M. J. Brown. 2021. Roundup causes high levels of mortality following contact exposure in bumble bees. *J. Appl. Ecol*. 58: 1167–1176.
Streinzer, M., and J. Spaethe. 2014. Functional morphology of the visual system and mating strategies in bumblebees (Hymenoptera, Apidae, *Bombus*). *Zool. J. Linn. Soc*. 170: 735–747.
Sutcliffe, G., and R. Plowright. 1988. The effects of food supply on adult size in the bumble bee *Bombus terricola Kirby* (Hymenoptera: Apidae). *Can. Entomol*. 120: 1051–1058.
Suzuki, K., I. Dohzono, and K. Hiei. 2007. Evolution of pollinator generalization in bumblebee-pollinated plants. *Plant Species Biol*. 22: 141–159.
Tasei, J.-N., and P. Aupinel. 2008. Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae). *Apidologie*. 39: 397–409.
Taylor, G. J., P. Tichit, M. D. Schmidt, A. J. Bodey, C. Rau, and E. Baird. 2019. Bumblebee visual allometry results in locally improved resolution and globally improved sensitivity. *Elife*. 8: e40613.
Theodorou, P., L. M. Baltz, R. J. Paxton, and A. Soro. 2020a. Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. *Evol. Appl*. 14: 53–68.
Thompson, H. M. 2001. Assessing the exposure and toxicity of pesticides to bumblebees (Bombus sp.). *Apidologie*. 32: 305–321.
Thomson, J. D. 1986. Pollen transport and deposition by bumble bees in Erythronium: influences of floral nectar and bee grooming. *J Ecol*. 74: 329–341.
Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*. 179: 90–92.
Van Doorn, A. 1989. Factors influencing dominance behaviour in queenless bumblebee workers (*Bombus terrestris*). *Physiol. Entomol*. 14: 211–221.
Van Dyck, H., and E. Matthysen. 1999. Habitat fragmentation and insect flight: a changing 'design'in a changing landscape? *Trends Ecol. Evol*. 14: 172–174.
Van Wyk, J. I., E. R. Amponsah, W. H. Ng, and L. S. Adler. 2021. Big bees spread disease: body size mediates transmission of a bumble bee pathogen. *Ecology*. 102: e03429.
Vanderplanck, M., R. Moerman, P. Rasmont, G. Lognay, B. Wathelet, R. Wattiez, and D. Michez. 2014. How does pollen chemistry impact development and feeding behaviour of polylectic bees? *PLoS One*. 9: e86209.
Vázquez, D. P., N. Blüthgen, L. Cagnolo, and N. P. Chacoff. 2009. Uniting pattern and process in plant–animal mutualistic networks: a review. *Ann. Bot. (Lond.)* 103: 1445–1457.
Vesterlund, S. -R., T. Lilley, T. Van Ooik, and J. Sorvari. 2014. The effect of overwintering temperature on the body energy reserves and phenoloxidase activity of bumblebee *Bombus lucorum* queens. *Insectes Soc*. 61: 265–272.
Vogt, F. D. 1986. Thermoregulation in bumblebee colonies. II. Behavioral and demographic variation throughout the colony cycle. *Physiol. Zool*. 59: 60–68.
Walton, A., J. Jandt, and A. Dornhaus. 2019. Guard bees are more likely to act as undertakers: variation in corpse removal in the bumble bee *Bombus impatiens*. *Insectes Soc*. 66: 533–541.
Weidenmüller, A., C. Kleineidam, and J. Tautz. 2002. Collective control of nest climate parameters in bumblebee colonies. *Anim. Behav*. 63: 1065–1071.
Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2006. Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia*. 149: 289–300.
Williams, P., S. Colla, and Z. Xie. 2009. Bumblebee vulnerability: common correlates of winners and losers across three continents. *Conserv. Biol*. 23: 931–940.
Williams, N. M., E. E. Crone, T. a. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv*. 143: 2280–2291.
Williams, P. H., R. W. Thorp, L. L. Richardson, and S. R. Colla. 2014. *Bumble bees of North America*. Princeton, NJ: Princeton University Press.
Williams, P. H., M. V. Berezin, S. G. Cannings, B. Cederberg, F. Ødegaard, C. Rasmussen, L. L. Richardson, J. Rykken, C. S. Sheffield, C. Thanoosing, *et al*. 2019. The arctic and alpine bumblebees of the subgenus *Alpinobombus* revised from integrative assessment of species' gene coalescents and morphology (Hymenoptera, Apidae, *Bombus*). *Zootaxa*. 4625: 1–68.
Willmer, P. G., and K. Finlayson. 2014. Big bees do a better job: intraspecific size variation influences pollination effectiveness. *J. Pollinat. Ecol*. 14: 244–254.
Winfree, R., I. Bartomeus, and D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Evol. Syst*. 42: 1–22.

Wood, T. J., G. Ghisbain, P. Rasmont, D. Kleijn, I. Raemakers, C. Praz, M. Killewald, J. Gibbs, K. Bobiwash, M. Boustani, ***et al*****. 2021**. Global patterns in bumble bee pollen collection show phylogenetic conservation of diet. *J. Anim. Ecol*. 90: 2421–2430.

Worden, B. D., A. K. Skemp, and D. R. Papaj. 2005. Learning in two contexts: the effects of interference and body size in bumblebees. *J. Exp. Biol*. 208: 2045–2053.

Wray, J. C., L. A. Neame, and E. Elle. 2014. Floral resources, body size, and surrounding landscape influence bee community assemblages in oak-savannah fragments. *Ecol. Entomol*. 39: 83–93.

Yerushalmi, S., S. Bodenhaimer, and G. Bloch. 2006. Developmentally determined attenuation in circadian rhythms links chronobiology to social organization in bees. *J. Exp. Biol*. 209: 1044–1051.

Zambra, E., B. Martinet, N. Brasero, D. Michez, and P. Rasmont. 2020. Hyperthermic stress resistance of bumblebee males: test case of Belgian species. *Apidologie*. 51: 911–920.

Zaragoza-Trello, C., M. Vilà, C. Botías, and I. Bartomeus. 2021. Interactions among global change pressures act in a non-additive way on bumblebee individuals and colonies. *Funct. Ecol*. 35: 420–434.

Zhao, H., S. K. Mashilingi, Y. Liu, and J. An. 2021a. Factors influencing the reproductive ability of male bees: current knowledge and further directions. *Insects*. 12: 529.

Zhao, H., Y. Liu, H. Zhang, T. D. Breeze, and J. An. 2021b. Worker-born males are smaller but have similar reproduction ability to queen-born males in bumblebees. *Insects*. 12: 1008.