



Bumble bee ecophysiology: integrating the changing environment and the organism

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Bumble bees are among the most ecologically and economically important pollinators worldwide, yet many of their populations are being threatened by a suite of interrelated, human-mediated environmental changes. Here, I discuss recent progress in our understanding of bumble bee ecophysiology, including advances related to thermal biology in light of global warming; nutritional biology in the context of declining food resources; and the capacity for bumble bees to exhibit physiological plasticity or adaptations to novel or extreme environments, with reference to their evolutionary history and current biogeography.

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Introduction

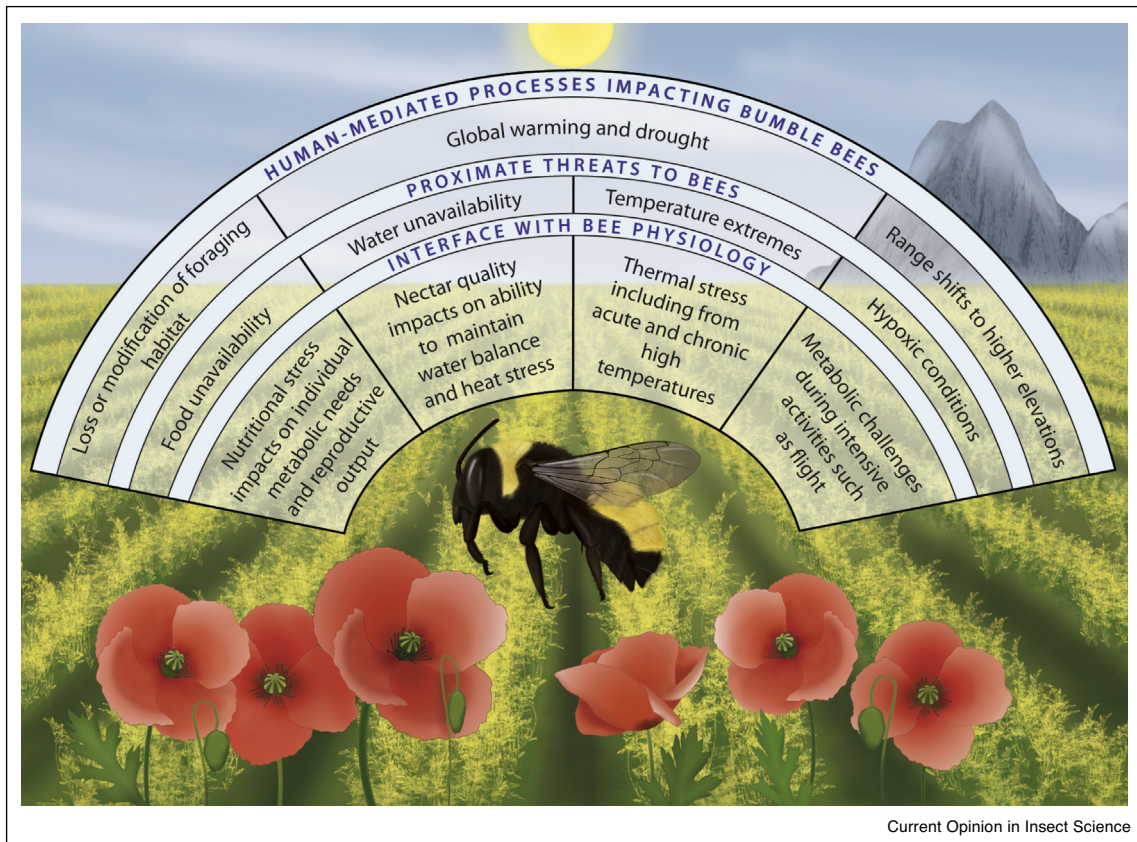
The extant bumble bees (genus *Bombus*, family Apidae) are a group of ~250 largely cold-adapted, relatively large-bodied bee species, with native species distributed widely throughout the Americas, Eurasia, and parts of Northern Africa [1,2]. Due to their primarily generalist foraging patterns, bumble bees have broad ecological importance in plant-pollinator networks, and the pollination services of a few species are intensively managed for commercial crop pollination in many parts of the world [3]. Bumble bees are also longstanding model systems in ecological and evolutionary research [4,5], and have recently emerged at the forefront of molecular research on non-*Apis* pollinators, with genomes published for two species and a variety of additional transcriptomic and other large molecular datasets available [6,7••].

Over the last decade, bumble bees have received considerable, growing attention related to human-mediated population declines and range shifts [8,9]. Although the group appears to have experienced substantial species losses prior

to the Anthropocene [10•], a growing body of evidence suggests that worldwide, some bumble bee populations are being increasingly threatened by factors associated with human activity, such as the intertwined effects of agricultural intensification and climate change [11,12]. Although there is no singular cause of bumble bee decline, and implicated factors appear to interact synergistically [11], the evidence that recent changes in habitat quality are a primary driver of bumble bee decline is particularly compelling. Bumble bees require suitable habitat for foraging, nesting, and for queen overwintering; among these, loss of foraging habitat has been studied most extensively, and its negative impacts on bumble bees have been demonstrated through a multitude of lines of evidence, including reduced survival of family lineages through time in areas with fewer floral resources [13••] and positive associations between food availability and the production of reproductives (queens and/or males) in wild [14], semi-wild [15], and laboratory [16] studies.

Implicit to many studies of bumble bee declines or range shifts, or even explicitly stated, is the assumption that these observed patterns are strongly or in part driven by the physiological limits of bumble bees (e.g., loss of species from the southern parts of their ranges due to limitations in upper thermal tolerance limits [12]). Yet, much remains unknown about bumble bee physiology and the true limits imposed by their environment, especially how this varies across the many bumble bee species and their respective ecological contexts. In the 1970s–90s, there were substantial advances in the field of bumble bee physiology, particularly in regard to flight physiology and thermoregulation [5]. This period was followed by a distinct decline in research in this area, with some exceptions, including continued laboratory work on endocrinology and neurobiology, particularly in the context of bumble bee sociobiology [17–20]. However, in recent years, there has been a resurgence of bumble bee physiological research, including examinations of how physiology functions with respect to ecologically relevant, dynamic conditions. This work is central to our understanding of bumble bee decline, in that it sheds light on how some of the broader forces that are negatively impacting bees, such as climate change, actually impact individual bee survival, reproduction, and other processes that are at the core of population health. This review focuses on this interface between bumble bee physiology and the human-mediated factors contributing to their decline (Figure 1), with an emphasis on the two areas of most rapid growth (thermal biology and nutrition), and

Figure 21



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Bumble bee physiology interfaces with human impacts. Major human impacts on bumble bees include the loss or alteration of foraging habitat, global warming and drought, and the human activity-induced movement of bumble bees to higher latitudes and elevations. These intertwined forces present ecological challenges for bumble bees that have direct physiological consequences; examples are shown here. Identifying how these challenges interface with bee physiology is essential for understanding the mechanistic basis of stressors involved in bumble bee decline. Artwork by A. Sanderson.

with the perspective that ecophysiology is among the most important research frontiers for generating insights into the fate of bumble bees in the face of global change.

Thermal biology: cold-adapted bees on a warming planet

The majority of the world's bumble bee species are found in Holarctic, alpine, or other temperate environments, and thus previously an emphasis has been placed on understanding bumble bee adaptations to the cold, such as thermoregulatory adaptations for foraging at relatively low ambient temperatures [21]. More recently, this emphasis has shifted toward their ability to tolerate the increasing ambient temperature conditions associated with global warming. Assessments of how individual bees are impacted by acute heat stress events have identified that bumble bees in the Holarctic subgenus *Alpinobombus* are more susceptible [22]. However, even heat-adapted subgenera living in areas with extreme summer temperatures might be threatened, particularly if queens emerge later in the year and more of their flight period occurs in

the height of summer [23]. Examinations of cold tolerance in *Bombus terrestris* have identified the first evidence for rapid cold hardening in bumble bees (in fact, in any Hymenoptera; [24,25]) and have identified that workers and, in particular, queens can survive acute cold periods if they become active during winter months [24]. Additional studies have explored critical thresholds of oxygen availability needed for thermoregulation [26], and upper and lower critical thermal limits of species found at different altitudes [27]. Queen and male bumble bees spend much of their life cycle removed from a social colony environment and without the benefit of colony-level thermoregulatory strategies, such as organized fanning behavior [28,29]. Thus, individual bumble bee thermoregulatory abilities are likely more important for males and perhaps even more so queens, who live much longer (up to nearly a year), including through a solitary overwintering period. Scriven and colleagues [30] have found support for this idea in the *B. lucorum* species complex, where queens and males, but not workers, follow Bergmann's rule, which states that larger-bodied individuals will be more

prevalent under cooler conditions due to thermoregulatory constraints [31]. Vesterlund and colleagues further examined queen thermoregulatory physiology in *B. lucorum* and found interactive effects with nutritional state, in that queens can survive longer under starvation conditions at lower temperatures [32], and that there are critical weight thresholds below which queens will not survive the period, irrespective of overwintering temperature conditions [33]. Young queens sequester substantial levels of lipids and glycogen in the fat body that they largely metabolize during the overwintering period [34,35], and interactive effects of nutrition and overwintering temperature may be related to a higher rate of metabolic processes under warmer temperature conditions, although this has not yet been demonstrated in bumble bees. Collectively, these studies speak to how bumble bee queens may fare more poorly, including in non-additive ways, in environments where both floral resource availability and abiotic conditions are undergoing major changes.

Drought, which is precipitated by warming conditions, also likely has direct and indirect negative impacts on bumble bee populations. Water balance is an understudied area in bee research, with additional complexity in social species where colony-level components should be considered, in addition to individual homeostasis (see [36] for a thorough review on this topic). The mechanisms underlying water balance in bumble bees deserve further study, as they are unique from honey bees and are almost certainly strained under drought conditions. For example, unlike honey bees, bumble bees typically do not forage for water (but see [37]), and thus obtain water for individual homeostasis from nectar, and they use dry fanning (i.e., without the evaporative method used by honey bees) as their primary means of cooling the colony. Drought impacts on floral resources is an emerging topic in pollinator research, and early work in this area suggests that in addition to directly limiting resource availability, there can also be more nuanced effects, such as changes in attractiveness to pollinators via altered plant volatile profiles [38] and impacts on competitive interactions between floral visitors [39].

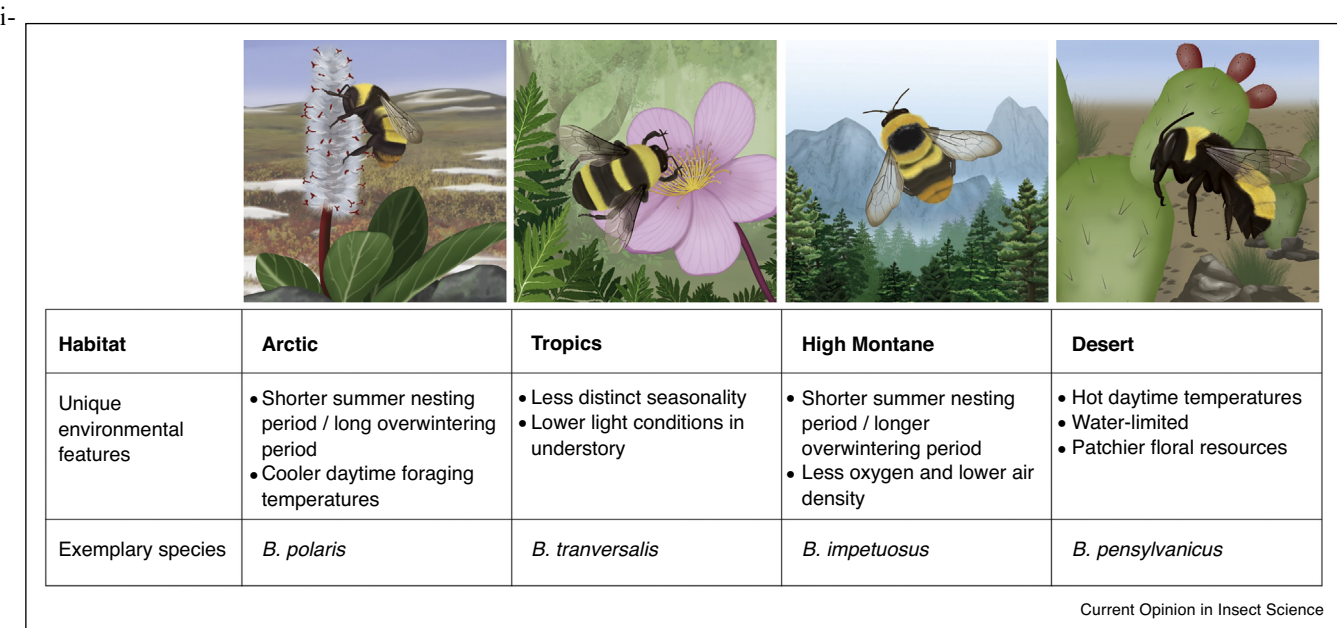
Nutritional biology of a generalist pollinator

Bee nutritional states are in part a function of the feeding-related decisions bees make, given the floral resources available in their surrounding landscape and the energy exerted for resource collection. Bumble bee nutritional biology is another rapidly expanding research area, which is being driven in part by the desire to use empirically-informed foraging habitat management practices that address foraging preferences and ultimately optimize bee health [40]. Bumble bees exhibit individual foraging preferences that are driven in part by direct assessments of floral rewards. Whereas earlier work focused largely on nectar valuation [5,41], the growing body of research in

this field has shifted focus to examine pollen, which is a compositionally more complex reward [42] (but see [43] for more recent work on nectar). These pollen-based studies have demonstrated that bumble bees may exhibit preferences for sweeter (vs. bitter) [44] and higher quality (vs. artificially modified with cellulose) [45] pollen, and may use their antennae to obtain chemotactile cues about pollen quality [46] and to differentiate between pollen from unique plant species [47^{••}]. As in other organisms [48], this decision-making process is partially dependent on nutritional state, and workers may feed preferentially to achieve nutrient balance with respect to relative amino acid profiles [49,50] and protein to lipid ratios [51,52^{••}]. Feeding-related decision making in bumble bees has also been examined in the context of non-nutritive food components. Research by Tiedekan et al. [53] has identified that bumble bees can taste and exhibit differential deterrence thresholds for unique nectar-derived secondary compounds, which complements work demonstrating that these compounds may be ingested to confer health benefits (e.g., self-medication against *Crithidia* infection; [54]). Interestingly, adult bumble bee workers may preferentially feed from nectar containing neonicotinoid insecticides, although this phenomenon appears to operate through effects on the nervous system (putatively, on nicotinic acetylcholine receptors) that do not involve primary components of taste-related neural circuitry [55^{••}].

Pollen availability is directly important for adult life stages in bumble bees, as adult workers consume pollen to the benefit of their health; for example, in *B. terrestris* [56] and *B. impatiens* [57], workers that are deprived of pollen and infected with the parasite *Crithidia* exhibit decreased immune responses and increased parasite loads, respectively. However, the consequences of worker foraging preferences are perhaps most relevant to the primary recipients of collected pollen: developing brood in the colony. Microcolony experiments have been used to demonstrate that polyfloral pollen diets and/or avoidance of particular monofloral pollen diets [58–62,63[•]], and pollen with higher amino acid concentrations [64,65], have positive effects on larval or colony development in *B. terrestris*, although work by Moerman and colleagues [66] demonstrating species-specific effects of diet on microcolony development suggests that these results in *B. terrestris* may not directly translate to other bumble bee species. A higher-level insight emerging from this work is that bumble bees tend to develop better (for example, more rapidly) when they consume pollen from multiple plant species, which is consistent with their largely generalist foraging habits. The corollary of this insight is that habitats with lower floral resource diversity do not optimally support bumble bees, and indeed this is what has been found repeatedly in field studies (e.g., [67,68]). In a complementary approach, researchers have also begun using metrics that are reflective of nutritional state (e.g.,

Figure 2



Bumble bees in extreme environments: models for anticipating responses to changing environments? Examples of bumble bees living in extreme environments (i.e., different from the temperate areas where most bumble bee species are found). Examples of characteristic features of each environment that are relevant to bumble bees are included and representative species are listed in the table and depicted in the images above. Artwork by A. Sanderson.

pid levels in bumble bees [69]; fat body mass in honey bees [70]) to investigate how land management practices interface with bee nutritional physiology. Now, a greater synthesis is needed between nutritional landscape ecology and bee physiology, in order to identify how bee nutrition is shaped by resource availability and floral preference, and to ultimately interpret the physiological significance of bee nutritional states.

Bumble bees in novel and extreme environments

The overwhelming majority of the world’s bumble bee species live in temperate zones and at altitudes up to or slightly above 5000 m, but there are some notable exceptions (Figure 2). For example, some bumble bee species (namely in the subgenus *Alpinobombus*) inhabit the Arctic, despite the dramatically lengthened overwintering period, shortened summer nesting season, and relatively cool (~5 °C) summer foraging temperatures in this region (although some of these features of the Arctic are dramatically changing; [71]). Research in the 1990s identified a key thermal strategy used by arctic queen bumble bees to persist under such extreme seasonality: the consistent upregulation of abdominal temperature, putatively for rapid ovary development upon emergence from overwintering; [72–74]. More recent work suggests that foragers can entrain their circadian clocks using UV light [75], which may aid in maintaining rhythmicity under the midnight sun, but additional adaptations

related to arctic inhabitation by bumble bees are currently unknown. Bumble bees are also found in subtropical and lowland tropical areas, where they may extend their nesting season and even nest perennially with multiple queens [76]; at high elevations, which may be more representative of ancestral conditions, and where flight abilities might be challenged [77*]; and in deserts, where extreme daytime temperatures may strongly shape foraging activity periods [78] to minimize water loss and heat stress, as is observed in other desert-dwelling bees [79].

The presence and persistence of bumble bees in these relatively unusual environments suggests that additional lineages within the extant bumble bee group may possess the plasticity or adaptive capability required for coping under similar environmental conditions. Thus, these species may serve as models for identifying the general capacity of bumble bees, which likely evolved in the cool, alpine Szechuan region of China [80,81], to modify their physiology in order to meet a wide variety of ecological challenges. However, most bumble bee lineages likely have more limited flexibility, given the relative rarity of bumble bees in these extreme environments, and the evidence that many declining populations are limited in their ability to undergo range shifts [12,82]. An exception is the small number of species that easily acclimate to vastly different environments, such as the heavily managed *B. terrestris*, which has been introduced in several parts of the world outside of its native range

(e.g., Chile and Argentina, Japan, New Zealand) and has since spread beyond introduction sites to new areas, a trend that is predicted to continue [83].

As the planet continues to become less hospitable for many pollinators [84], and less like the original ecological conditions under which the bumble bee lineage arose [80,81], the physiological flexibility of bumble bees will become increasingly important for their persistence, either in their current environments or as they move to inhabit new areas. Some bumble bee populations already appear to be shifting northward, such as the movement of Scandinavian populations of *B. terrestris* and *B. lapidarius* north of the Arctic Circle [85]; other populations appear limited in their ability for northward movement, despite contractions at the southern parts of their ranges [12]. Other populations appear to be moving to higher elevations [12,86,87], where they may inhabit montane refugia that are more buffered from human impacts. Lower oxygen levels and lower air density make insect flight more challenging at higher altitudes (reviewed in [88]), although experimental transplants of bumble bees to elevations higher than they naturally occur suggest some flexibility for upward movement, despite these challenges [77*]. Recent work on bumble bee flight metabolism and respiration [89–92] and flight biomechanics (e.g., [93–95]) dually contributes to our understanding of the basic biology of bumble bees, and also how the metabolic and mechanical challenges associated with movement to higher elevations might be met by upwardly-migrating populations. Under both latitudinal and altitudinal movement scenarios, bumble bees may encounter new challenges as they crowd into refugia, such as greater competition with congenics and other bee groups as they converge on similar floral resources [96–98], or the spread of disease-related microorganisms to new areas and between and within newly-assembled bee communities [99,100]. For example, the human-facilitated spread of *B. terrestris* into South America has been linked to both of these phenomena, which appear to be drivers in the decline of the native species *B. dahlbomii* in this region [99,101,102]. Continued explorations of bumble bee physiology and competitive interactions under dynamic, field-realistic conditions are critical for anticipating the outcomes of these scenarios, and for managing habitat to ameliorate negative impacts on bumble bee populations.

Conclusion

Bumble bees face a variety of human-mediated threats; ecophysiological research is critical for understanding their susceptibility and resilience to these pressures, and for modeling how populations will respond to changing ecological conditions. Recent advances in bumble bee ecophysiological research, which focuses on organismal function, can complement studies in the fields of pollination biology and landscape and community ecology, by

shedding light on the underlying physiological mechanisms that shape ecosystem-level patterns and processes. A key area of future progress is an improved understanding of how thermal biology, nutrition, and other classic components of insect ecophysiological research [103] integrate and act synergistically with other environmental stressors that are historically outside of the scope of ecophysiology. This will include, for example, examining how the detoxification and immune response machinery in bumble bees, which have been identified via genome sequencing [7**] and functional genomic studies [104,105], operate as a function of thermal conditions and bee nutritional state. Disease-causing organisms and pesticides have been strongly implicated in the decline of bumble bees (reviewed in [11,106]). However, research on these factors has focused primarily on prevalence and effects of exposure on mortality and colony development, respectively, and less on their physiological effects (but see [107] for an examination of how pesticide exposure impacts bumble bee queen ovary development, and [108] for an exemplary study addressing combined effects of pesticides and pathogens on queen detoxification- and immune-related enzyme activities in honey bees). Another important research area is the integration of bumble bee sociobiology with ecophysiology, to explore how the social environment inside the nest and the foraging environment interact to shape physiological processes. Ongoing advances in this area are a necessary and timely component of the effort to identify and predict how our changing planet will continue to impact this enormously important pollinator group.

Conflicts of interest

I wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Cameron SA, Hines HM, Williams PH: **A comprehensive phylogeny of the bumble bees (*Bombus*)**. *Biol J Linn Soc* 2007, **91**:161–188.
 2. Williams PH: **An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini)**. *Bull Nat Hist Mus Lond (Entomol)* 1998, **67**:79–152.
 3. Velthuis HHW, Van Doorn A: **A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination**. *Apidologie* 2006, **37**:421–451.

4. Goulson D: *Bumblebees*. Oxford University Press on Demand; 2010.
5. Heinrich B: *Bumblebee Economics*. Harvard University Press; 2004.
6. Woodard SH, Lozier JD, Goulson D, Williams PH, Strange JP, Jha S: **Molecular tools and bumble bees: revealing hidden details of ecology and evolution in a model system**. *Mol Ecol* 2015, **24**:2916-2936.
7. Sadd BM, Barribeau SM, Bloch G, de Graaf DC, Dearden P, Elsik CG, Gadau J, Grimmekhuijzen CJP, Hasselmann M, Lozier JD *et al.*: **The genomes of two key bumblebee species with primitive eusocial organization**. *Genome Biol* 2015, **16**:76.
- Describes the first two bumble bee genomes to be sequenced (*B. impatiens* and *B. terrestris*), including similarities and differences in genome content in comparison to honey bees (*A. mellifera*) and other Hymenoptera.
8. Goulson D, Lye GC, Darvill B: **Decline and conservation of bumble bees**. *Annu Rev Entomol* 2008, **53**:191-208.
9. Williams PH, Osborne JL: **Bumblebee vulnerability and conservation world-wide**. *Apidologie* 2009, **40**:367-387.
10. Condamine FL, Hines HM: **Historical species losses in bumblebee evolution**. *Biol Lett* 2015, **11**:20141049.
- Estimates historical gains and losses of bumble bee species, providing insight into how the group may have been shaped by periods of intensive climatic changes prior to the present
11. Goulson D, Nicholls E, Botías C, Rotheray EL: **Bee declines driven by combined stress from parasites, pesticides, and lack of flowers**. *Science* 2015, **347**:1255-1257.
12. Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, Rasmont P, Schweigher O, Colla SR, Richardson LL, Wagner DL, Gall LF, Sikes DS, Patoja A: **Climate change impacts on bumblebees converge across continents**. *Science* 2015, **349**:177-180.
13. Carvell C, Bourke AFG, Dreier S, Freeman SN, Hulmes S, Jordan WC, Redhead JW, Sumner S, Wang J, Heard MS: **Bumblebee family lineage survival is enhanced in high-quality landscapes**. *Nature* 2017, **40**:367.
- The first study to use genetic approaches to examine how habitat quality impacts the survival of bumble bee lineages through time, from when summer workers are present, through the overwintering stage, to the spring queen stage. Flower cover was among the variables most strongly associated with lineage persistence, suggesting that floral resource availability is a major limiting factor for bumble bee survival.
14. Rundlöf M, Persson AS, Smith HG, Bommarco R: **Late-season mass-flowering red clover increases bumble bee queen and male densities**. *Biol Conserv* 2014, **172**:138-145.
15. Crone EE, Williams NM: **Bumble bee colony dynamics: quantifying the importance of land use and floral resources for colony growth and queen production**. *Ecol Lett* 2016, **19**:460-468.
16. Rotheray EL, Osborne JL, Goulson D: **Quantifying the food requirements and effects of food stress on bumble bee colony development**. *J Api Res* 2017, **51**:1-11.
17. Shpigler H, Amsalem E, Huang ZY, Cohen M, Siegel AJ, Hefetz A, Bloch G: **Gonadotropic and physiological junctions of juvenile hormone in bumblebee (*Bombus terrestris*) workers**. *PLoS ONE* 2014, **9**:e100650-e100710.
18. Amsalem E, Malka O, Grozinger C, Hefetz A: **Exploring the role of juvenile hormone and vitellogenin in reproduction and social behavior in bumble bees**. *BMC Evol Biol* 2014, **14**:45.
19. Jedlička P, Ernst UR, Votavová A, Hanus R, Valterová I: **Gene expression dynamics in major endocrine regulatory pathways along the transition from solitary to social life in a bumblebee, *Bombus terrestris***. *Front Physiol* 2016, **7**:574.
20. Woodard SH, Bloch G, Band MR, Robinson GE: **Social regulation of maternal traits in nest-founding bumble bee (*Bombus terrestris*) queens**. *J Exp Biol* 2013, **216**:3474-3482.
21. Heinrich B: **Temperature regulation in the bumblebee *Bombus vagans*: a field study**. *Science* 1972, **175**:185-187.
22. Martinet B, Lecocq T, Smet J, Rasmont P: **A protocol to assess insect resistance to heat waves, applied to bumblebees (*Bombus Latreille*, 1802)**. *PLoS ONE* 2015, **10**:e0118591.
23. Rasmont P, Iserbyt S: **The bumblebees scarcity syndrome: are heat waves leading to local extinctions of bumblebees (Hymenoptera: Apidae: *Bombus*)?** *Ann Soc Entomol Fr* 2012, **48**: Taylor & Francis Group, 2012.
24. Owen EL, Bale JS, Hayward SAL: **Can winter-active bumblebees survive the cold? Assessing the cold tolerance of *Bombus terrestris audax* and the effects of pollen feeding**. *PLoS ONE* 2013, **8**:e80061.
25. Owen EL, Bale JS, Hayward SAL: **Establishment risk of the commercially imported bumblebee *Bombus terrestris dalmatinus*-can they survive UK winters?** *Apidologie* 2016, **47**:66-75.
26. Dzialowski EM, Tattersall GJ, Nicol SC, Frappell PB: **Fluctuations in oxygen influence facultative endothermy in bumblebees**. *J Exp Biol* 2014, **217**:3834-3842.
27. Oyen KJ, Giri S, Dillon ME: **Altitudinal variation in bumble bee (*Bombus*) critical thermal limits**. *J Therm Biol* 2016, **59**:52-57.
28. Westhus C, Kleineidam CJ, Rocas F, Weidenmüller A: **Behavioural plasticity in the fanning response of bumblebee workers: impact of experience and rate of temperature change**. *Anim Behav* 2013, **85**:27-34.
29. Jandt JM, Dornhaus A: **Bumblebee response thresholds and body size: does worker diversity increase colony performance?** *Anim Behav* 2014, **87**:97-106.
30. Scriven JJ, Whitehorn PR, Goulson D, Tinsley MC: **Bergmann's body size rule operates in facultatively endothermic insects: evidence from a complex of cryptic bumblebee species**. *PLoS ONE* 2016, **11**:e0163307.
31. Bergmann C: **About the relationships between heat conservation and body size of animals**. *Goett Stud* 1847, **1**:595-708.
32. Vesterlund S-R, Sorvari J: **Longevity of starved bumblebee queens (Hymenoptera: Apidae) is shorter at high than low temperatures**. *Eur J Entomol* 2014, **111**:1-5.
33. Vesterlund SR, Lilley TM, van Ooik T, Sorvari J: **The effect of overwintering temperature on the body energy reserves and phenoloxidase activity of bumblebee *Bombus lucorum* queens**. *Insect Soc* 2014, **61**:265-272.
34. Amsalem E, Galbraith DA, Cnaani J, Teal PEA, Grozinger CM: **Conservation and modification of genetic and physiological toolkits underpinning diapause in bumble bee queens**. *Mol Ecol* 2015, **24**:5596-5615.
35. Votavová A, Tomčala A, Kofroňová E, Kudzejová M, obotník J, Jiro P, Komzáková O, Valterová I: **Seasonal dynamics in the chemistry and structure of the fat bodies of bumblebee queens**. *PLoS ONE* 2015, **10**:e0142261-e142314.
36. Nicolson SW: **Water homeostasis in bees, with the emphasis on sociality**. *J Exp Biol* 2009, **212**:429-434.
37. Ferry C, Corbet SA: **Water collection by bumble bees**. *J Apicultural Res* 1996, **35**:120-122.
38. Burkle LA, Runyon JB: **Drought and leaf herbivory influence floral volatiles and pollinator attraction**. *Global Change Biol* 2016, **22**:1644-1654.
39. Thomson DM: **Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources**. *Ecol Lett* 2016, **19**:1247-1255.
40. Vaudo AD, Tooker JF, Grozinger CM: **Bee nutrition and floral resource restoration**. *Curr Opin Ins Sci* 2015, **10**:133-141.
41. Heinrich B: **Energetics of pollination**. *Annu Rev Ecol Evol Syst* 1975, **6**:139-170.
42. Roulston TH, Cane JH: **Pollen nutritional content and digestibility for animals**. *Plant Syst Evol* 2000, **222**:187-209.

43. Mommaerts V, Wackers F, Smagghe G: **Assessment of gustatory responses to different sugars in harnessed and free-moving bumblebee workers (*Bombus terrestris*)**. *Chem Senses* 2013, **38**:399-407.
44. Muth F, Francis JS, Leonard AS: **Bees use the taste of pollen to determine which flowers to visit**. *Biol Lett* 2016, **12**:20160356.
45. Ruedenauer FA, Spaethe J, Leonhardt SD: **Hungry for quality—individual bumblebees forage flexibly to collect high-quality pollen**. *Behav Ecol Sociobiol* 2016, **70**:1209-1217.
46. Ruedenauer FA, Spaethe J, Leonhardt SD: **How to know which food is good for you: bumblebees use taste to discriminate between different concentrations of food differing in nutrient content**. *J Exp Biol* 2015, **218**:2233-2240.
47. Ruedenauer FA, Leonhardt SD, Schmalz F, Rössler W, Strube-
• Bloss MF: **Separation of different pollen types by chemotactile sensing in *Bombus terrestris***. *J Exp Biol* 2017, jeb-153122..
Found evidence that antennal contact with different pollen types (apple vs almond) elicits unique electroantennographic responses in the bumble bee *B. terrestris*, providing additional support that chemotactile cues are used to assess and differentiate between pollens, and suggesting that differentiation involves distinct patterns of receptor neuron activity in the antennae.
48. Wright GA: **To feed or not to feed: circuits involved in the control of feeding in insects**. *Curr Opin Neurobiol* 2016, **41**:87-91.
49. Kriesell L, Hilpert A, Leonhardt SD: **Different but the same: bumblebee species collect pollen of different plant sources but similar amino acid profiles**. *Apidologie* 2017, **48**:102-116.
50. Stabler D, Paoli PP, Nicolson SW, Wright GA: **Nutrient balancing of the adult worker bumblebee (*Bombus terrestris*) depends on the dietary source of essential amino acids**. *J Exp Biol* 2015, **218**:793-802.
51. Vaudo AD, Stabler D, Patch HM, Tooker JF, Grozinger CM, Wright GA: **Bumble bees regulate their intake of the essential protein and lipid pollen macronutrients**. *J Exp Biol* 2016, **219**:3962-3970.
52. Vaudo AD, Patch HM, Mortensen DA, Tooker JF, Grozinger CM:
• **Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies and floral preferences**. *Proc Natl Acad Sci USA* 2016, **113**:E4035-E4042.
Found that bumble bee workers consistently forage for pollen with higher protein to lipid ratios, across a series of semi-wild and cage experiments, suggesting that relative macronutrient content of pollen is a major component driving bumble bee foraging preferences.
53. Tiedeken EJ, Stout JC, Stevenson PC, Wright GA: **Bumblebees are not deterred by ecologically relevant concentrations of nectar toxins**. *J Exp Biol* 2014, **217**:1620-1625.
54. Richardson LL, Adler LS, Leonard AS, Andicoechea J, Regan KH, Anthony WE, Manson JS, Irwin RE: **Secondary metabolites in floral nectar reduce parasite infections in bumblebees**. *Proc Biol Sci Lond B* 2015, **282**:20142471.
55. Kessler SC, Tiedeken EJ, Simcock KL, Derveau S, Mitchell J,
• Softley S, Stout JC, Wright GA: **Bees prefer foods containing neonicotinoid pesticides**. *Nature* 2015, **521**:74-76.
Demonstrated that bumble bees are not deterred from feeding on sugar solutions containing nectar-relevant levels of neonicotinoid pesticides, and may even preferentially feed on them. This suggests that, at a minimum, bumble bees cannot actively avoid nectar with these pesticides, and may increase their exposure via their own feeding preferences.
56. Brunner FS, Schmid-Hempel P, Barribeau SM: **Protein-poor diet reduces host-specific immune gene expression in *Bombus terrestris***. *Proc Biol Sci Lond B* 2014, **281**:20140128.
57. Conroy TJ, Palmer-Young EC, Irwin RE, Adler LS: **Food limitation affects parasite load and survival of *Bombus impatiens* (Hymenoptera: Apidae) infected with *Crithidia* (Trypanosomatida: Trypanosomatidae)**. *Environ Entomol* 2016, **45**:1212-1219.
58. Tasei J-N, Aupinel P: **Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae)**. *Apidologie* 2008, **39**:397-409.
59. Moerman R, Vanderplanck M, Fournier D, Jacquemart A-L, Michez D: **Pollen nutrients better explain bumblebee colony development than pollen diversity**. *Insect Conserv Diversity* 2017, **10**:171-179.
60. Genissel A, Aupinel P, Bressac C, Tasei JN, Chevrier C: **Influence of pollen origin on performance of *Bombus terrestris* microcolonies**. *Entomol Exp Appl* 2002, **104**:329-336.
61. Vanderplanck M, Moerman R, Rasmont P, Lognay G, Wathelet B, Wattiez R, Michez D: **How does pollen chemistry impact development and feeding behaviour of polylectic bees?** *PLoS ONE* 2014, **9**:e86209.
62. Vanderplanck M, Declèves S, Roger N: **Is non-host pollen suitable for generalist bumblebees?** *Insect Sci* 2016, **00**:1-14.
63. Roger N, Michez D, Wattiez R, Sheridan C, Vanderplanck M: **Diet • effects on bumblebee health**. *J Insect Physiol* 2017, **96**:128-133.
Used microcolonies fed three different monofloral diets, varying in nutritional quality, to examine connections between nutritional stress and multiple metrics that are reflective of bumble bee health. Determined that negative effects of pollen diet can be detected in both brood (e.g., lower mass) and adult workers (e.g., higher prophenoloxidase activity).
64. Moerman R, Vanderplanck M, Roger N, Declèves S, Wathelet B, Rasmont P, Fournier D, Michez D: **Growth rate of bumblebee larvae is related to pollen amino acids**. *J Econ Entomol* 2016, **109**:25-30.
65. Baloglu GH, Gurel F: **The effects of pollen protein content on colony development of the bumblebee, *Bombus terrestris* L.** *J Api Sci* 2015, **59**:83-88.
66. Moerman R, Roger N, De Jonghe R, Michez D, Vanderplanck M: **Interspecific variation in bumblebee performance on pollen diet: new insights for mitigation strategies**. *PLoS ONE* 2016, **11**:e0168462.
67. Jha S, Kremen C: **Resource diversity and landscape-level homogeneity drive native bee foraging**. *Proc Natl Acad Sci USA* 2013, **110**:555-558.
68. Hülsmann M, Wehrden von H, Klein A-M, Leonhardt SD: **Plant diversity and composition compensate for negative effects of urbanization on foraging bumble bees**. *Apidologie* 2015, **46**:760-770.
69. Smith GW, Debinski DM, Scavo NA, Lange CJ, Delaney JT, Moranz E, Miller JR, Engle DM, Toth AL: **Bee abundance and nutritional status in relation to grassland management practices in an agricultural landscape**. *Environ Entomol* 2016, **45**:338-347.
70. Alaux C, Allier F, Decourtye A, Odoux JF, Tarnic T, Chabirand M, Delestra E, Decugis F, Le Conte Y, Henry M: **A 'Landscape physiology' approach for assessing bee health highlights the benefits of floral landscape enrichment and semi-natural habitats**. *Scientific Reports* 2017, **7**:40568.
71. *Arctic Report Card*. Richter-Menge J, Overland JE, Mathis JT. 2016. <http://www.arctic.noaa.gov/Report-Card>.
72. Heinrich B, Vogt FD: **Abdominal temperature regulation by arctic bumblebees**. *Physiol Zool* 1993, **66**:257-269.
73. Vogt FD, Heinrich B, Dabolt TO: **Ovary development and colony founding in subarctic and temperate-zone bumblebee queens**. *Can J Zool* 1994, **72**:1551-1556.
74. Vogt FD, Heinrich B, Plowright C: **Ovary development in bumble bee queens: the influence of abdominal temperature and food availability**. *Can J Zool* 1998, **76**:2026-2030.
75. Chittka L, Stelzer RJ, Stanewsky R: **Daily changes in ultraviolet light levels can synchronize the circadian clock of bumblebees (*Bombus terrestris*)**. *Chronobiol Int* 2013, **30**:434-442.
76. Sakagami SF: **Specific differences in the bionomic characters of bumblebees. A comparative review**. *J Fac Sci Hokkaido Univ Zool* 1976, **20**:390-447.
77. Dillon ME, Dudley R: **Surpassing Mt. Everest: extreme flight performance of alpine bumble-bees**. *Biol Lett* 2014, **10**:20130922-20130922.

Used experimental transplants to demonstrate that bumble bees are capable of sustained flight at altitudes greater than 9000 m, which speaks to their potential for colonizing high elevation areas

78. Shelly TE, Buchmann SL, Villalobos EM, O'Rourke MK: **Colony ergonomics for a desert-dwelling bumblebee species (Hymenoptera, Apidae)**. *Ecol Entomol* 1991, **16**:361-370.
79. Willmer P, Stone G: **Temperature and water relations in desert bees**. *J Thermal Biol* 1997, **22**:453-465.
80. Hines HM: **Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera: Apidae: *Bombus*)**. *Syst Biol* 2008, **57**:58-75.
81. Williams PH, Bystrakova N, Huang J: **Bumblebees, climate and glaciers across the Tibetan plateau (Apidae: *Bombus* Latreille)**. *Syst Biodivers* 2015, **13**:164-181.
82. Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, Griswold TL: **Patterns of widespread decline in North American bumble bees**. *Proc Natl Acad Sci USA* 2011, **108**:662-667.
83. Acosta AL, Giannini TC, Imperatriz-Fonseca VL, Saraiva AM: **Worldwide alien invasion: a methodological approach to forecast the potential spread of a highly invasive pollinator**. *PLoS ONE* 2016, **11**:e0148295-e148325.
84. Settele J, Bishop J, Potts SG: **Climate change impacts on pollination**. *Nat Plants* 2016, **2**:16092.
85. Martinet B, Rasmont P, Cederberg B: **Forward to the north: two Euro-Mediterranean bumblebee species now cross the Arctic Circle**. *Ann Soc entomol Fr* 2015, **51** Taylor & Francis Group, 2015.
86. Pyke GH, Thomson JD, Inouye DW, Miller TJ: **Effects of climate change on phenologies and distributions of bumble bees and the plants they visit**. *Ecosphere* 2016, **7**:e01267.
87. Ploquin EF, Herrera JM, Obeso JR: **Bumblebee community homogenization after uphill shifts in montane areas of northern Spain**. *Oecologia* 2013, **173**:1649-1660.
88. Dillon ME, Frazier MR, Dudley R: **Into thin air: physiology and evolution of alpine insects**. *Int Comp Biol* 2006, **46**:49-61.
89. Darveau C-A, Billardon F, Bélanger K: **Intraspecific variation in flight metabolic rate in the bumblebee *Bombus impatiens*: repeatability and functional determinants in workers and drones**. *J Exp Biol* 2014, **217**:536-544.
90. Skandalis DA, Darveau C-A: **Morphological and physiological idiosyncrasies lead to interindividual variation in flight metabolic rate in worker bumblebees (*Bombus impatiens*)**. *Physiol Biochem Zool* 2012, **85**:657-670.
91. Vogt JR, Dillon ME: **Allometric scaling of tracheal morphology among bumblebee sisters (Apidae: *Bombus*): compensation for oxygen limitation at large body sizes?** *Physiol Biochem Zool* 2013, **86**:576-587.
92. Vogt JR, Dillon MK, Dillon ME: **Tracheole investment does not vary with body size among bumblebee (*Bombus impatiens*) sisters**. *Comp Biochem Physiol A Mol Integr Physiol* 2014, **174**:56-61.
93. Mountcastle AM, Ravi S, Combes SA: **Nectar vs. pollen loading affects the tradeoff between flight stability and maneuverability in bumblebees**. *Proc Natl Acad Sci USA* 2015, **112**:10527-10532.
94. Chang JJ, Crall JD, Combes SA: **Wind alters landing dynamics in bumblebees**. *J Exp Biol* 2016, **219**:2819-2822.
95. Ravi S, Kolomenskiy D, Engels T, Schneider K, Wang C, Sesterhenn J, Liu H: **Bumblebees minimize control challenges by combining active and passive modes in unsteady winds**. *Scientific Reports* 2016, **6**:35043.
96. Miller-Struttmann NE, Geib JC, Franklin JD, Kevan PG, Holdo RM, Ebert-May D, Lynn AM, Kettenbach JA, Hedrick E, Galen C: **Functional mismatch in a bumble bee pollination mutualism under climate change**. *Science* 2015, **349**:1541-1544.
97. Miller-Struttmann NE, Galen C: **High-altitude multi-taskers: bumble bee food plant use broadens along an altitudinal productivity gradient**. *Oecologia* 2014, **176**:1033-1045.
98. Pradervand JN, Pellissier L: **Functional homogenization of bumblebee communities in alpine landscapes under projected climate change**. *Climate Change Responses* 2014, **1**:1.
99. Arbetman MP, Meeus I, Morales CL, Aizen MA, Smagghe G: **Alien parasite hitchhikes to Patagonia on invasive bumblebee**. *Biol Invasions* 2012, **15**:489-494.
100. Cameron SA, Lim HC, Lozier JD, Duennes MA, Thorp R: **Test of the invasive pathogen hypothesis of bumble bee decline in North America**. *Proc Natl Acad Sci USA* 2016, **113**:4386-4391.
101. Schmid-Hempel R, Eckhardt M, Goulson D, Heinzmann D, Lange C, Plischuk S, Escudero LR, Salathé R, Scriven JJ, Schmid-Hempel P: **The invasion of southern South America by imported bumblebees and associated parasites**. *J Anim Ecol* 2014, **83**:823-837.
102. Morales CL, Arbetman MP, Cameron SA, Aizen MA: **Rapid ecological replacement of a native bumble bee by invasive species**. *Front Ecol Environ* 2013, **11**:529-534.
103. Harrison JF, Woods A, Roberts SP: *Ecological and environmental physiology of insects*. Oxford University Press; 2010.
104. Xu J, Strange JP, Welker DL, James RR: **Detoxification and stress response genes expressed in a western North American bumble bee, *Bombus huntii* (Hymenoptera: Apidae)**. *BMC Genomics* 2013:14.
105. Samson-Robert O, Labrie G, Mercier P-L, Chagnon M, Derome N, Fournier V: **Increased acetylcholinesterase expression in bumble bees during neonicotinoid-coated corn sowing**. *Scientific Rep* 2015, **5**:1-8.
106. Meeus I, Brown MJF, de Graaf DC, Smagghe G: **Effects of invasive parasites on bumble bee declines**. *Conservation Biol* 2011, **25**:662-671.
107. Baron GL, Raine NE, Brown MJF: **General and species-specific impacts of a neonicotinoid insecticide on the ovary development and feeding of wild bumblebee queens**. *Proc Roy Soc Lond B* 2017, **284**:20170123.
108. Dussaubat C, Maisonnasse A, Crauser D, Tchamitchian S, Bonnet M, Cousin M, Kretzschmar A, Brunet J-L, Le Conte Y: **Combined neonicotinoid pesticide and parasite stress alter honeybee queens' physiology and survival**. *Scientific Reports* 2016, **6**:31430.