Why is sex good and asexuality bad? It is widely accepted that sexual reproduction is favoured because of genetic recombination, which makes natural selection much more efficient, unless you have enormous population sizes. Asexuality does not generate the genetic variation — the new combinations of alleles within and across chromosomes — that recombination does, and in the evolutionary long-term, asexual lineages are more prone to extinction than sexual lineages.

That does sound bad. So, when is sex bad and asexuality good? The main cost of sex is the so-called ‘two-fold cost of males’. Females directly produce offspring, whereas males invest minimally in offspring, often only providing genetic material. Thus, asexual females should generate twice as many offspring as sexual females, who waste half their resources on the production of males. Of course, in some species males do positively contribute to offspring through parental care, but the time and energy spent searching for mates, the risk of failing to mate, and the increased risk of predation or sexually transmitted diseases all make sex a costly venture. Asexuality avoids these costs and maximises offspring production. So, a species that manages some sex and some asexual reproduction, like facultatively parthenogenetic species, should get the benefits of both. Indeed, theory suggests having only a little sex goes a long way.

That means the real question is: why aren’t all organisms facultatively parthenogenetic?! Exactly! And while it is no doubt true that the prevalence of facultative parthenogenesis is likely to be underestimated, given it is so hard to detect in nature, it is clearly not as common as we might think it should be. Certainly, the developmental constraints of initiating embryonic development *de novo* may be substantial, and the long-term benefits for sexual lineages and their subsequent evolution may have meant that going back to asexuality has become impossible. The evolution of genomic imprinting associated with mammalian embryonic development may be one example of this. But recently a new idea has been put forward that might help us understand why facultative parthenogenesis may come and go.

Do tell! One factor that may be shaping the evolution of facultative parthenogenesis is sexual conflict over mating. Males and females may often disagree over mating decisions, with coercion or mating struggles taking place prior to copulation. Recent theory suggests that facultative parthenogenesis can intensify sexual conflict over mating, generating stronger selection for both male coercion and female resistance. If females can evolve effective resistance to males and the costs of resistance do not outweigh the benefits of asexual reproduction, resistance could facilitate the evolution of parthenogenesis. However, if males ‘win’ the sexual conflict, male coercion could prevent females reproducing parthenogenetically, constraining the evolution of facultative strategies and helping to explain the persistence of obligate sex. Understanding whether and how sexual conflict over matings influence facultative parthenogenesis is an exciting new avenue to be explored.

Where can I find out more?

Burke, N.W., and Bonduriansky, R. (2017). Sexual conflict, facultative asexuality, and the true paradox of sex. Trends Ecol. Evol. *32*, 646–652.
D’Souza, T.G., and Michiels, N.K. (2010). The costs and benefits of occasional sex: Theoretical predictions and a case study. J. Hered. *101*, S34–S41.
Lehtonen, J., Jennions, M.D., and Kokko, H. (2012). The many costs of sex. Trends Ecol. Evol. *27*, 172–178.
Morgan-Richards, M., Langton-Myers, S.S., and Trewick, S.A. (2019). Loss and gain of sexual reproduction in the same stick insect. Mol. Ecol. *28*, 3929–3941.
Sperling, A.L., and Glover, D.M. (2023). Parthenogenesis in dipterans: A genetic perspective. Proc. R. Soc. B *290*, 20230261.
van der Kooi, C.J., and Schwander, T. (2015). Parthenogenesis: Birth of a new lineage or reproductive accident? Curr. Biol. *25*, R659–R661.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Department of Biology, University of St Andrews, Harold Mitchell Building, St Andrews KY16 9TH, UK.
*E-mail: david.shuker@st-andrews.ac.uk

Primer

Bumblebees

Guillaume Ghisbain[1,*],
Lars Chittka[2], and Denis Michez[1]

Few stinging insects inspire as much warm affection as bumblebees. This group of social, furry, and colorful bees, all comprised within the genus *Bombus* Latreille, are among the most abundant pollinators in cold or temperate ecosystems, and act as key vectors for the pollination of both wild and cultivated flowering plants. The buzzing flight from flower to flower of these large, noisy insects never fails to capture the attention of children, nature lovers, and also professional entomologists. In his book *The Effects of Cross & Self-Fertilisation in the Vegetable Kingdom*, Charles Darwin himself made numerous observations on the intelligent floral visitation of “humble bees” (as they were called at the time), which led him to consider them as “...*good botanists*, *for they know that varieties may differ widely in the colour of their flowers and yet belong to the same species*”. Further fascinated about bumblebee behaviour and their faculty to pierce holes in flowers for robbing nectar, he suggested, in a letter for the *Gardner’s Chronicle* in 1841, “*...that the practice of boring holes in* [...] *flowers is likewise a piece of acquired knowledge*”. The very tangible consequence of bumblebees’ visibility today is their remarkable representation in entomological collections. Museums worldwide are filled with millions of pinned specimens, collected since the 18th century, collectively serving as invaluable witnesses to how insect communities have changed over time. Bumblebees have become flagship species for insect conservation — especially conservation of pollinators — and have shaped our understanding of how current anthropogenic changes impact the animals upon which we depend for our well-being and the resilience of terrestrial ecosystems. In this Primer, we present a beginner’s guide to the behavior, biogeography, conservation, ecology and evolution of these highly studied pollinators.

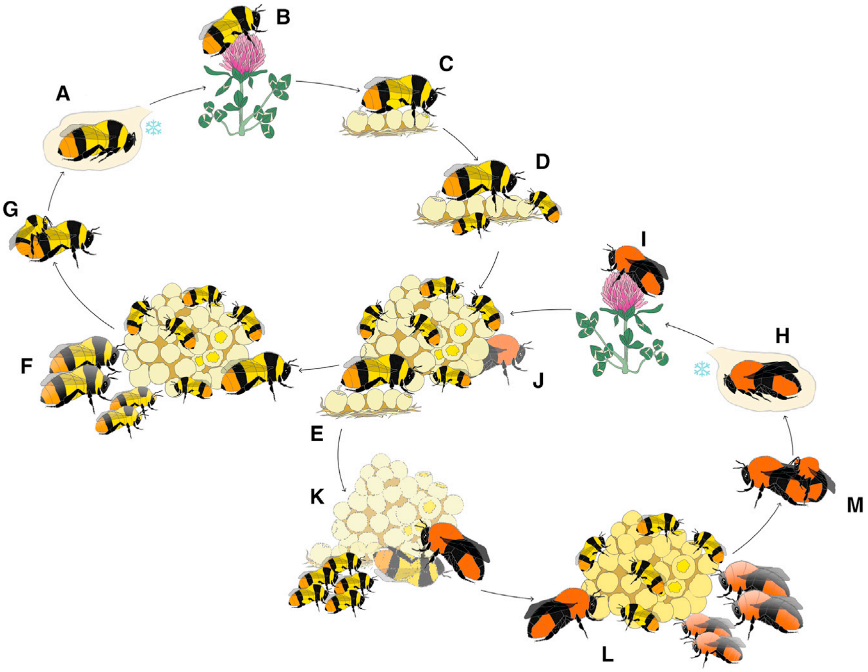

Figure 1. Interconnected life cycles of a free-living host bumblebee species (A–G) and its associated cuckoo species (H–M).

(A) Queen hibernating; (B) queen feeding; (C) queen founding its colony; (D,E) colony developing with workers; (F) emergence of males and young queens (lighter individuals on the left); (G) mating of a young queen and male; (H) cuckoo queen hibernating; (I) cuckoo queen feeding; (J) cuckoo queen hidden in the colony of its host; (K) cuckoo queen killing the host queen; (L) host workers now working for the cuckoo queen, and emergence of cuckoo males and young cuckoo queens (lighter individuals on the right); (M) mating of a young cuckoo queen and cuckoo male. The depicted colors for bumblebee hairs are for illustration purposes only and are not based on an actual host–parasite species pair. (Figure by Olympe Tritto.)

Origin and radiation

Molecular and morphological evidence demonstrates that bumblebees, within the family Apidae, are included in the ‘corbiculate Apidae’, which, as the name suggests, includes bees that show corbiculae (pollen baskets) on their hind legs. This clade also includes three other social groups, the familiar honeybees (*Apis* spp.) and stingless bees (tribe Meliponini) — both known for their production of honey — as well as the tropical orchid bees (tribe Euglossini).

The history of bumblebees likely began between 40 and 25 million years ago, during a global cooling event, near the Eocene–Oligocene boundary, probably in Asia, where most of the early-diverging clades and the highest species diversity still occur today. Recent insights on bumblebee history and biogeography suggest that the expansion of the arid desert region across Central Asia around 34 million years ago was an early critical step for their evolution. This is evidenced by the fact that species of the earliest-diverging extant bumblebee subgenera are concentrated either in the mountains south of this uninhabitable desert, or in the hills to the north. After 21 million years ago, the subsequent re-activation of the uplift of the Pamir and Tian Shan mountain ranges might have provided a climatically and ecologically suitable bridge for dispersal and faunal exchange of the descendants of these early-diverging bumblebees. Dispersal from Asia to Europe likely occurred around 11 million years ago for the lowland, long-faced bumblebee fauna and around 5 million years ago for the montane, short-faced bumblebees. To the East, some lineages spread to North America through Beringia when land connections allowed, and reached Central America around 8–12 million years ago. It is likely that some species colonized South America around 3 million years ago, where some endemic species exist today.

Life cycle and eusociality

While the vast majority of bees are solitary, all representatives of the genus *Bombus* are either eusocial (Figure 1A–G) or inquiline (i.e. social parasites exploiting the colony of another bumblebee species; Figure 1H–M and Box 1). Each colony is initiated by a foundress queen, a large fertilized female that establishes her nest in various locations depending on the species — at the ground level within vegetation, underground in old rodent burrows or cavities, and more rarely in trees or bird nests. The egg-laying process invariably begins with fertilized (diploid) eggs, which will continue to be produced regularly over the next several months. The queen first forages by herself on pollen and nectar to feed the first larvae, which develop as smaller females called workers. Bumblebee colonies are caste-differentiated, with both the queen and workers involved in maintaining the colony’s cohesion, security, temperature, health and development. The reproductive behavior of bumblebee workers is plastic: until a so-called ‘competition point’ in which new queen production has been initiated by the queen, workers typically refrain from laying their own eggs while retaining functional ovarioles. Colony social and hierarchical cues, including physical intimidation and/or pheromone manipulation from the queen, or self-regulation in a given social context (e.g., queen presence and quality), could act as informative signals that indirectly affect the physiology, ovariole activation and behavior of workers.

Remarkably, bumblebees have been interpreted as ‘hot-blooded insects’ (endothermic heterotherms) — both the queen and workers are capable of generating endogenous metabolic heat to incubate the brood. This thermogenic process, provided by facultative endothermy, can occur during active flight, but also when stationary.

Most late-spring and summer bumblebees are workers that are actively collecting nectar and pollen, the only two food resources used by bumblebees globally. Pollen is mostly collected for providing larvae with the proteins and lipids necessary for their development, while nectar is consumed by both adults and larvae, mostly providing carbohydrates. Some floral

Box 1. The socially parasitic ‘cuckoo bumblebees’.

Parasitism is among the most common lifestyles on earth. In social insects, the substantial cost of brood care has favored the emergence of socially parasitic species that infiltrate the nest of other species to force the host to rear their offspring. Around a tenth of the global extant species diversity of bumblebees are obligate social parasites, or inquilines, with females that are neither capable of founding their own nests nor collecting pollen. This lifestyle is shared by — but not restricted to — all species of the workerless subgenus *Psithyrus*, in which parasitic females invade already developed nests and utilize the host workers to care for their own offspring (Figure 1H–M). After an initial estimation of nest quality (identity of the host, stage of development), these so-called ‘cuckoo bumblebees’ either avoid contact with the hosts and hide to acquire the odor of the colony, secrete a repellent molecule to protect themselves from worker attacks, or immediately attack any individual hostile to them. The parasitic female then integrates the host social system, which is in some species facilitated by mimicking the chemical profile of the host’s cuticle. The host queen is generally eliminated, after which the cuckoo feeds on the eggs and destroys the brood of the host. The reproduction of the host workers is inhibited by a combination of aggressive behavior and production of chemicals that hinder the development of their ovaries. The rest of the life cycle resembles that of free-living bumblebees but without the production of new workers: only queens and males are produced and these individuals then reproduce in the wild. Fertilized cuckoo females finally find a hibernaculum to survive through winter, before the cycle repeats itself in the next year. Note that emerging queens of typically free-living species have also been observed usurping the nests of other bumblebee species in a similar fashion.

resources are also rich in secondary metabolites with various properties, such as antioxidants, antibacterial, or antiparasitic. Many bumblebee species are generalists whose interactions with flowers are largely shaped by learning. This means that, out of the dozens of plant species available in any nest’s flight range (these can strongly vary among bee species and habitats), bees sample the nectar and pollen rewards of multiple species, and then memorize the colors, patterns and scents of the ones experienced as most rewarding, and subsequently focus their foraging efforts on these plant species while disregarding others. Since many flower structures such as snapdragons or monkshoods are natural ‘puzzle boxes’, their manipulation must be learned over individuals’ lifetimes, to hone the most efficient physical skills to get to the nectar. The extraction of pollen — typically a powdery substance with grains of various sizes and shapes — is more complex still, and requires learning how and from which body parts to groom the grains and how to pack them efficiently into the pollen baskets. This complexity, along with the diverse possible chemical compositions of pollen, might be one reason that the range of flower species used as pollen sources is narrower in some bumblebee species than for nectar — the complexity of pollen foraging perhaps favoring innate skills and corresponding digestive physiology to process only particular kinds of pollen.

These flower foraging skills have made bumblebees into key models for studies of animal intelligence, and the question of how much cognition can be mediated with how small a brain (Figure 2). As opposed to these behaviorally flexible generalists, a handful of bumblebee species are characterized as ‘oligolectic’, meaning they consume a very limited diversity of floral resources for feeding their larvae (Figure 2B). Such species have sacrificed the learning flexibility required to be a food generalist for the advantage of not having to sample multiple flower species and learning to handle them. The risks, however, are obvious: to the extent that intelligence can buffer survival under man-made duress, such specialists will suffer first in conditions when, for example, climate change produces a desynchronisation of the flowering of their plant species and the bees’ phenology.

Males (usually haploid individuals produced by either the aging queen or unfertilized workers) and new virgin queens (diploid individuals solely produced by the aging queen) emerge towards the end of the colony’s life and do not normally participate in colony organization, though they occasionally participate in warming the brood in some species. The time at which the aging queen switches from laying diploid eggs yielding females to laying haploid eggs yielding males is typically referred to as the ‘switch point’. Males usually quit the nest a few days after emergence when their pheromone glands are fully developed and start looking for newly emerged queens.

Males commonly patrol a familiar area in which they search for queens: they mark stones, branches or leaves with secretions — produced by their cephalic labial glands — used as pheromones to attract virgin queens. Other mating behavior strategies have been described, such as waiting by nest entrances (i.e., males wait for virgin queens to emerge from their nest) and perching (i.e., males wait on prominent objects to visually detect and approach virgin queens). Unlike honeybee drones, which die after mating, male bumblebees can mate with multiple queens sequentially. Males transfer a gelatinous product of their accessory glands called the ‘mating plug’ to the female, which prevents the female from further mating. Neither workers, males or the queen of the previous year hibernate — all die before winter.

In most species, the newly emerged queens only mate with a single male individual and, after mating, hibernate alone in a little soil cavity called a ‘hibernaculum’. The life cycle of bumblebees can dramatically differ in tropical regions where no cold or dry season is marked. For instance, mild winter seasons in southern Brazil can allow perennial foraging and nest initiation in *Bombus atratus*, with gynes not entering diapause. Nests of this species can continue for several generations, with a fraction of inseminated gynes coming back to their natal nest to start a new cycle when the older queen dies. This system involves cyclical polygyny, with multiple reproductive queens fighting until the expulsion or death of all but one of them.

Bumblebees as models of animal intelligence

The behavioral flexibility of bumblebees is likely rooted in their lifestyle as flower visitors, which requires learning the locations of the flowers relative to the nest, their visual and olfactory displays, and the motor skills to handle the flowers (Figure 2A,B). In the laboratory, bumblebees display cognitive abilities that were previously thought to be the prerogative of large-brained vertebrates. They can learn to open complex puzzle boxes (Figure 2C; where the red tab needs to be rotated to align with the yellow field to obtain a sugar reward, but the blue tab needs to be moved out of the way first, to allow movement of the red tab). Such skills can be learned by observation from skilled conspecifics. Bumblebees can also learn to roll balls to a particular destination to secure a reward, in a manner that equates to simple tool use (Figure 2D). Moreover, even when food rewards are not present, bees will repeatedly roll balls, indicating a form of play behavior, and possibly an emotional state of enjoyment. They display cross-modal recognition, indicating that they have mental images of objects. Bumblebees trained to recognise the visual appearance of one shape (balls) from another (cubes) (Figure 2E) can subsequently recognise these same shapes in complete darkness from touch alone (shown under infrared light; Figure 2F).

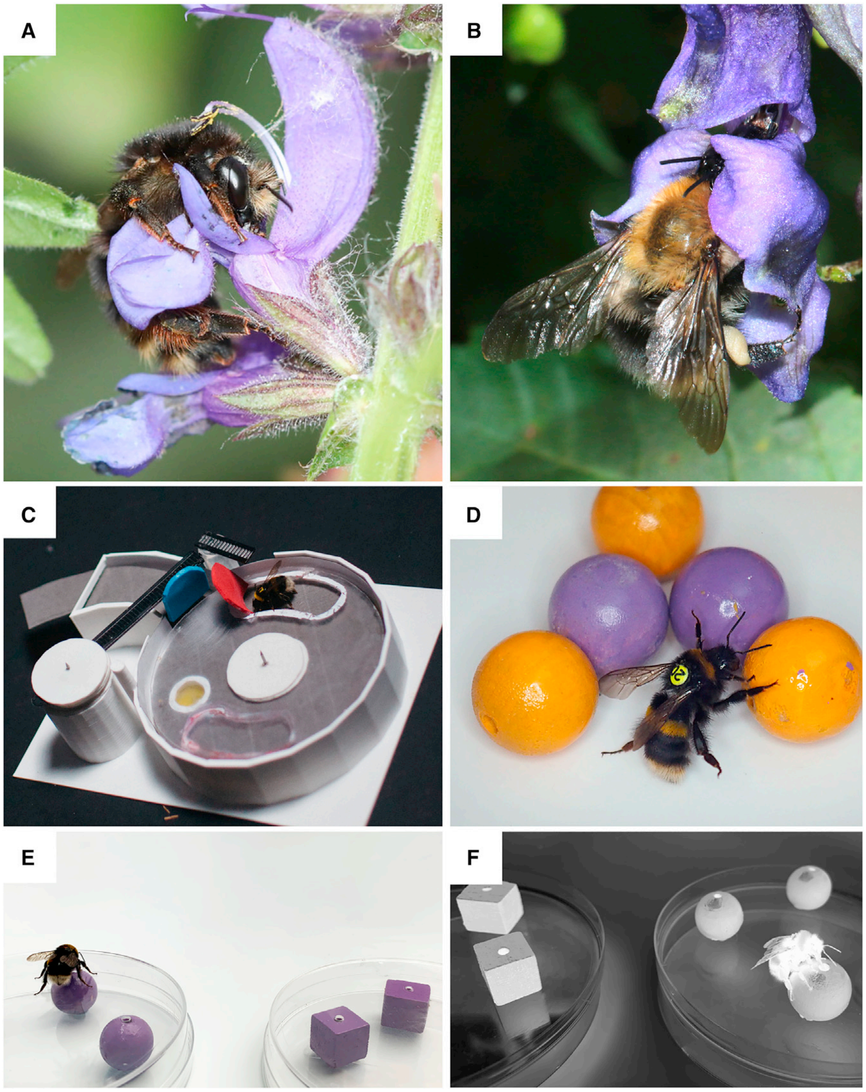

Figure 2. Bumblebee intelligence in the wild and in the lab.
(A,B) Bumblebees handling flowers with a complex morphology to access nectar; (A) *Bombus humilis* on a *Salvia pratensis*; (B) *B. gerstaeckeri* is an obligatory specialist on plants of the genus *Aconitum* (here, *A. napellus*; note the extended proboscis for reaching the deep nectaries). (C) A worker of *B. terrestris* learning to open a complex puzzle box. (D) Workers of *B. terrestris* roll balls for enjoyment and can also learn to roll a ball to a goal to secure a reward, thus using the ball as a tool. (E,F) A female of *B. terrestris* trained to recognise the visual appearance of a sphere from a cube (E) and subsequently recognising these same shapes from touch alone in complete darkness (F). Photo credits: (A) Sophie Giriens, (B) Volkmar Nix, (C) Stefan Hanegraaf, (D) Richard Rickitt, and (E,F) Lars Chittka.

A complex phenotypic radiation

One remarkable hallmark of bumblebees is their profusion of colors (Figure 3). Even though there are only around 300 recognized species globally, thousands of color patterns have been described historically as species, subspecies, varieties, forms, morphs or even ‘aberrations’. It is thus not uncommon to find a bright orange bumblebee specimen and an almost entirely dark specimen that are actually conspecific, passing through dozens of different color forms throughout the geographical distribution of the species. *Bombus pascuorum*, ranked amongst the most abundant European species, is a perfect example of intraspecific variation, which can make the species arduous to identify and separate from similarly colored species (e.g., *B. humilis, B. muscorum*). The pronounced variation in color coat between bumblebee species, local populations and even within populations captured the attention of evolutionary biologists early in the 20th century, and made these bees key models for studying evolutionary divergence and convergence, adaptation, and genetic drift.

The drivers that explain the local convergence of several sympatric species towards similar color patterns include Müllerian mimicry, in which coexisting unpalatable species or those with stingers evolve a similar appearance to reduce the mortality involved in training predators to avoid them. Geographic phenotypic variation should therefore be analyzed in relation to the sympatric species communities. Apart from mimicry, camouflage and thermoregulation are cited as other, likely context-dependent, mechanisms for understanding intraspecific variation in bumblebees. The physical impact of color on thermoregulation in bumblebees is a largely overlooked, yet exciting avenue of research, especially in the context of climate change. Counterintuitively, the darkest species are most frequently found in the tropics, and not in higher latitude areas where light absorption by dark hairs could be interpreted as advantageous for warming up in cooler environments.

Despite their astonishing diversity of colors, the exoskeletal morphology

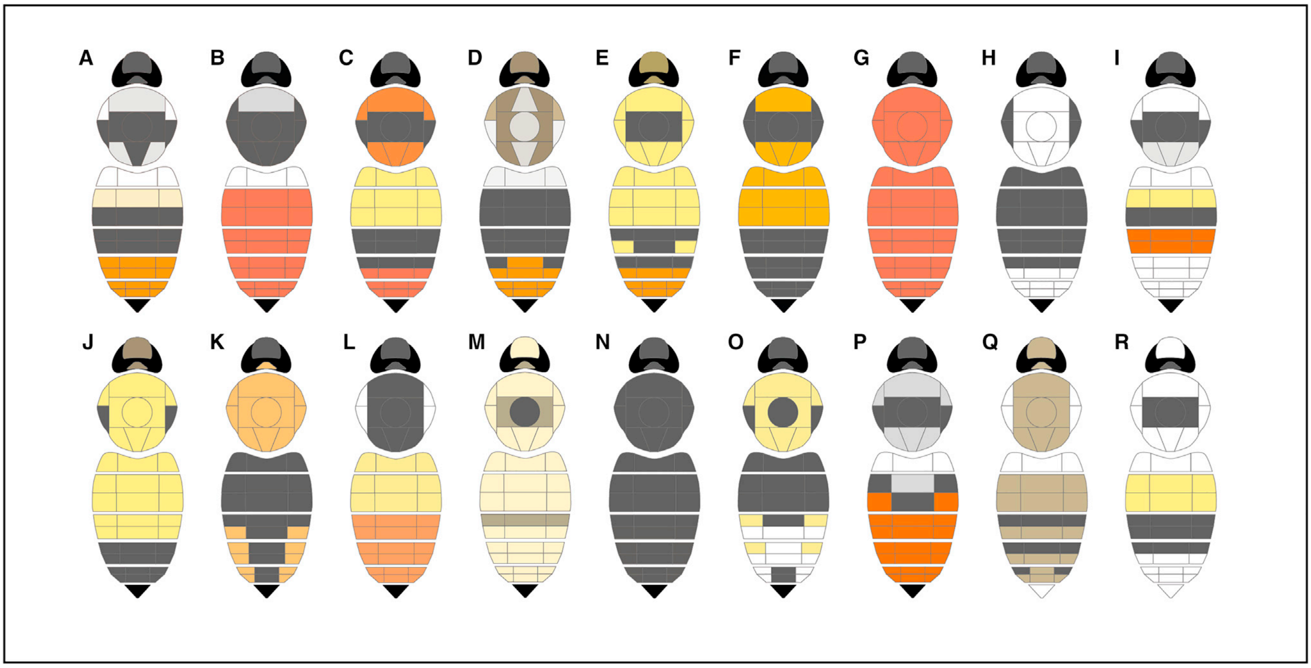

Figure 3. The colorful phenotypic radiation of bumblebees.
Species were selected solely as examples illustrating the immense diversity in color patterns within the genus: (A) *Bombus sikkimi*; (B) *B. validus*; (C) *B. breviceps*; (D) *B. grahami*; (E) *B. kirbiellus*; (F) *B. hyperboreus*; (G) *B. morawitzi*; (H) *B. festivus*; (I) *B. rufofasciatus*; (J) *B. nevadensis*; (K) *B. ferganicus*; (L) *B. albopleuralis*; (M) *B. keriensis*; (N) *B. flavescens*; (O) *B. bohemicus*; (P) *B. formosellus*; (Q) *B. infrequens*; and (R) *B. patagiatus*. Color diagrams inspired by the works of Paul H. Williams, bumblebee specialist at the National History Museum (London, England).

of phylogenetically distant bumblebee species can appear largely monotonous compared with that of many other bee clades. Species delineation therefore has proven challenging in this group compared with other bee clades. As a result, bumblebee taxonomists had to develop complementary species concepts (e.g., ecological, semio-chemical or phylogenetic). Besides commonly used mitochondrial and nuclear markers for building phylogenies, genome-level analyses have been applied in bumblebee populations to explore gene flow between putatively different species. Mounting evidence also suggests that many bumblebee species can be differentiated by the profile of the cephalic labial gland secretions of the males. Some taxa can also be differentiated based on their wing shape through geometric morphometrics, an approach that has been used to revise cryptic fossil and type material for which no alteration of specimens is possible for genetic-level analyses. Given all these advances, it is no surprise that the taxonomy, and especially integrative taxonomy, of these pollinators is the most thoroughly developed among all wild bee genera globally.

Sensitivity to global changes

One of the reasons why bumblebees have become an increasingly hot topic in the last decades is because of issues related to their conservation. Bumblebee populations in the Northern Hemisphere, particularly in Europe and North America, have drastically declined since the Second World War. A comparison of a collection of bumblebees from the early 20th century with specimens collected at similar locations and seasons reveals, in many cases, a decrease in the relative abundance of certain species, their extirpation, or even their extinction. In Europe, the only continent where a Red List has been published for the entire bee fauna, bumblebees unambiguously appeared as a particularly imperiled group, with >25% of the species threatened with extinction. The reasons for this decline are multiple, but many mechanisms underlying this decline are intuitive and well understood.

The primary drivers of bumblebee decline, as with insects in general, stem from intensive land use by human societies, particularly habitat change through the pervasive spread of industrialized agriculture dominating entire landscapes. More particularly, drastic changes in land use were often associated with the decline of plant species belonging to the legume family (Fabaceae). Historically in Europe, multiple species of clover (*Trifolium* spp.), alfalfa (*Medicago sativa*), or common sainfoin (*Onobrychis viciifolia*) were widely used as green manure to re-enrich fields with nitrogen. The advent of chemical fertilizers, produced and sold on a large scale from the first half of the 20th century through the Haber-Bosch synthesis process, had two major consequences on agriculture and on bumblebees. It first made the use of legumes for soil enrichment obsolete, but also excessively enriched the soil with nitrates and phosphates. The eutrophication phenomenon resulting from this massive use of chemical fertilizers has profoundly impacted global biogeochemical cycles, especially that of nitrogen, with profound consequences on the plant communities available to bumblebees and other pollinators. Plant species that are not tolerant to these industrial molecules in soils are now much less common, to the point where the availability of these plants has become limiting for maintaining bumblebee populations in many regions.

In addition to being impoverished in high-quality floral resources, agricultural and industrialized regions expose bumblebees to various pesticides, including herbicides, fungicides, and insecticides, but also other hazards including microplastics (and released phthalates) and trace metals. Beyond their direct lethal impacts, field-realistic acute or chronic exposure to these toxic compounds can cause sublethal effects, including disruption of their behavior (e.g., cognition, food intake or flight abilities), alteration of their morphology (e.g., body size) or fecundity, that ultimately contribute to reduce individual and colony fitness. As in other animals, it is likely that intelligence could act as a first line of defense against man-made global change. Higher levels of behavioral flexibility will enable the exploitation of novel food sources, using unusual nesting sites and materials, and utilizing man-made landmarks as navigational aids in fragmented habitats. Yet neurotoxic pesticides threaten the brain-mediated versatility that allows some species of bumblebees to thrive despite a variety of other anthropogenic stressors. This problem is accentuated by the fact that bumblebees are not necessarily able to avoid or identify these toxic compounds at field-realistic concentrations, which ultimately leads to their ingestion.

Between-species differences in behavioral flexibility of bumblebees (such as between flower generalists and specialists) likely explain, at least in part, why some species are in decline, while others still thrive even in the face of substantial man-made adversity. The key European model of bumblebee intelligence in research laboratories, the large earth bumblebee (*Bombus terrestris*), is indeed rapidly spreading to many habitats where it is not native. Its domestication in the 1980s and subsequent global trade for crop pollination led to acute patterns of invasion in several regions of the world. Documented impacts of this geographical expansion include pathogen spill-over to native bumblebee populations, competition for nesting and floral resources and hybridization with local closely related bumblebee taxa. National regulations already prevent the introduction of *B. terrestris* into mainland Australia and the United States of America, and Japan lists it as a major invasive species. Urgent coordinated species importation policies are critically needed for some South American countries such as Chile and Argentina, where *B. terrestris* (and another exported European species, *B. ruderatus*) strongly contributed to the decline of the largest bumblebee of the world, *B. dahlbomii,* the sole species endemic to Patagonia.

The decline of certain bumblebee species can also be well explained by an inherent physiological limitation: the overwhelming majority of bumblebees are sensitive to heat. Individuals show particular vulnerability to heatwaves, which are becoming longer, more frequent, and more intense in a context of climate change. In addition to extreme climatic events, the current alteration of climate involves a slower, yet significant increase in surface temperatures, resulting in species distribution range shifts among bumblebees.

Rather than viewing these causes of decline as independent, one must understand that bumblebees are generally subjected to multiple, sometimes concomitant anthropogenic stresses throughout their lives. A bumblebee born today in an area with highly degraded landscape will spend most of its life cycle in fragmented habitats with scarce and poor-quality resources, polluted with xenobiotics, and has an increasing risk of experiencing at least one heatwave during its lifetime. Models projecting future continental-scale ecological suitability under various land use and climate change scenarios are clear in their message: mitigation policies are urgently needed to protect these vulnerable pollinators from further human-driven transformations of the biosphere.

Conclusions

Despite being among the most extensively studied bees worldwide, we are only at the dawn of understanding the intricate universe of bumblebees. Promising research avenues — such as the exploration of their cognitive agility, their sophisticated selection and management of resources, the origins of their sociality, and their spectacular evolutionary radiation — are still in their infancy. Furthermore, as emerging threats like novel pollutants and climate extremes continue to reshape ecosystems, deciphering how bumblebees navigate and endure mounting environmental stressors has become crucial for predicting their population trends. Future research on the mechanisms underlying their decline and resilience will be key to developing conservation strategies that not only ensure species persistence but also safeguard their vital ecological functions. The choices we make today will decide whether future generations have the privilege of discovering these marvels with the same admiration we do — or if bumblebees will become just another case study in the annals of a world reshaped by human progress.

DECLARATION OF INTERESTS

The authors declare no competing interests.

FURTHER READING

Bridges, A.D., Royka, A., Wilson, T., Lockwood, C., Richter, J., Juusola, M., and Chittka, L. (2024). Bumblebees socially learn behaviour too complex to innovate alone. Nature *627*, 572–578. https://doi.org/10.1038/s41586-024-07126-4.

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

Chittka, L. (2022). The Mind of a Bee (Princeton, NJ: Princeton University Press).

Galpayage Dona, H.S., Solvi, C., Kowaleska, A., Makel, K., MaBouDi, H., and Chittka, L. (2022). Do bumble bees play? Anim. Behav. *119*, 239–251. http://doi.org/10.1016/j.anbehav.2022.08.013.

Ghisbain, G., Thiery, W., Massonnet, F., Erazo, D., Rasmont, P., Michez, D., and Dellicour, S. (2024). Projected decline in European bumblebee populations in the twenty-first century. Nature *628*, 337–341.

Goulson, D., Lye, G.C., and Darvill, B. (2008). Decline and conservation of bumble bees. Annu. Rev. Entomol. *53*, 191–208.

Raine, N.E., and Rundlöf, M. (2024). Pesticide exposure and effects on non-*Apis* bees. Annu. Rev. Entomol. *69*, 551–576.

Rasmont, P., Ghisbain, G., and Terzo, M. (2021). Bumblebees of Europe and Neighbouring Regions (Verrières-le-Buisson: NAP Editions), p. 632.

Velthuis, H.H.W., and van Doorn, A. (2006). A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. Apidologie *37*, 421–451.

Williams, P. (2007). The distribution of bumblebee colour patterns worldwide: Possible significance for thermoregulation, crypsis, and warning mimicry. Biol. J. Linn. Soc. *92*, 97–118.

Williams, P.H. (2022). The Bumblebees of the Himalaya: An Identification Guide (Brussels: ABC Taxa), p. 202.

Williams, P.H. (2023). Can biogeography help bumblebee conservation? Eur. J. Taxon. *890*, 165–183.

[1]Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Place du Parc 20, 7000 Mons, Belgium. [2]School of Biological and Behavioural Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK.
*E-mail: Guillaume.GHISBAIN@umons.ac.be