Apidologie (2025) 56:19
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https://doi.org/10.1007/s13592-024-01138-9

Review article

Why bumblebees have become model species in apidology: A brief history and perspectives

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Received 13 May 2024 – Revised 19 November 2024 – Accepted 5 December 2024

Abstract – In recent years, bumblebees have increasingly been used to study various aspects of bee biology, ecology and evolution. They are now broadly accepted as tractable model species, complementary to the domestic honey bees, for fundamental and applied apidology. Here, we provide a brief history of how bumblebee research developed since their domestication and commercialisation for crop pollination in the 1990s. Bumblebees are large social bees that can be kept and trained in the lab year-round. They are easy to manipulate and track individually in their small colonies. These practical advantages have offered new possibilities for experimental bee research, leading to major breakthroughs in different fields such as cognition, navigation, nutrition, host-parasite interactions, and insect declines. Many of these findings have later been confirmed in honey bees and other pollinators. We discuss some exciting directions for future apidology research based on bumblebees.

Bumble bees / *Bombus terrestris* / *Bombus impatiens* / *Bombus ignitus* / Cognition / Navigation / Nutrition / Host-parasite interactions

1. INTRODUCTION

Bee research has historically been developed on, and is still largely dominated by, studies on honey bees (Figure 1). This is understandable given the thousands of years of domestication of honey bees and the many commercial benefits they generate for hive products and crop pollination. Beyond apidology, experimental observations on honey bees have led to discoveries of fundamental importance in animal behaviour and ecology. Over the past century or so, James Turner, Karl von Frisch, Mathilde Hertz, Martin Lindauer, Randolf Menzel, Tom Seeley and many other famous bee biologists, have described the impressively rich behavioural and cognitive repertoire of honey bees, supporting a sophisticated and efficient social organization in small-brained animals. This long history of research on honey bees has raised these fascinating social insects to the level of model organisms for many areas of insect science, including behaviour (Giurfa 2007), neurosciences (Menzel 2012), physiology (Wang et al. 2018), nutrition (Wright et al. 2018), and social evolution (Woodard et al. 2015).

Yet, honey bees are quite unique among bees and insects in general. They represent just a dozen of the 20,000 species of bees described so far (Michener 2000), and display sophisticated

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Manuscript editor: James Nieh.

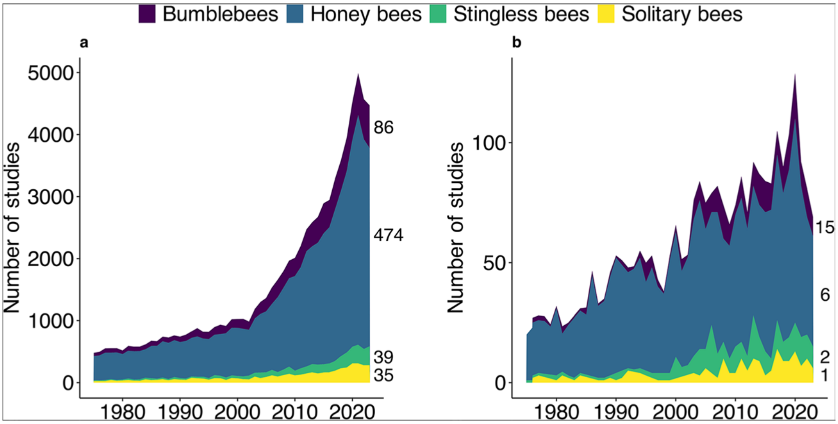

Figure 1. Numbers of studies published yearly per categories of bee species. (**a**) In all scientific journals. (**b**) In the journal *Apidologie*. Number of studies published in 2024 are displayed on the right next to graphs. Articles in English published between 1975 and 2024 were searched on ISI Web of Knowledge database (search performed on 17/03/2024 using keywords: insect and honey bee and *Apis*; stingless bee or *Melipona*; solitary bee or leafcutter or *Osmia* or carpenter; bumblebee or *Bombus*).

behaviours associated with extreme levels of social organization and division of labour that are not found in most bee species. One can indeed question the relevance of focusing all research efforts on one or two model species only (i.e. *Apis mellifera* Linnaeus, 1758 and *A. cerana* Fabricius, 1793) to study a broad group of animals (Hunter 2008). The majority of bee species live in much simpler colonies with a flexible division of labour, or are not social at all (Wilson and Hölldobler 2005). Bees are found in most terrestrial environments and thus show behavioural and physiological adaptations that cannot always be investigated using honey bees. In particular, most bee species do not actively recruit conspecifics to food resources or nest sites through a dance, and must instead explore and learn to exploit resources of their environment by themselves (Giurfa 2015). There is thus a need to diversify bee models in order to build a broader vision about their biology and ecology as a whole.

Accordingly, over the recent years, bumblebees have increasingly been used for bee research. Bumblebees is a large group of eusocial bees composed of approximately 260 species grouped within 15 subgenera (Williams et al. 2008). These large bees are primarily found in the Northern Hemisphere but also in South America (Frison 1925). Like honey bees, bumblebees have long intrigued naturalists. Darwin explained how he was fascinated by the routing behaviour of male bumblebees looking for females (Freeman 1968) and Bennett (1883) and Christy (1883) described how individual bumblebees specialised in visiting certain flower species when foraging. However, these observations were mainly descriptive and opportunistic due to the difficulty to raise bumblebee colonies and use them to experimentally test hypotheses.

Breeding of wild-caught bumblebee colonies for scientific research was achieved since the beginning of the twentieth century and led to fundamentally important lines of research in behavioural and pollination ecology (see for instance studies by Aubrey Manning, Anne Brian, Graham Pyke, Robert Plowright). But bumblebee research really took a significant expansion in the 1990s, thanks to mass breeding with the professional domestication and commercialization of bumblebee hives for greenhouse pollination (for a review see Velthuis and van Doorn 2006). From this moment, an increasing number of bee researchers used bumblebees in experimental programs. This made pre-existing lines of research accessible to investigators who had not mastered the techniques of starting their own colonies or harvesting nests from the field. Commercial availability democratized the field to non-specialists, and it also allowed specialists to work year-round and far more efficiently. Bumblebees appeared particularly suitable for experimental work as they can be tested in the field and in the lab using homemade setups (e.g. mazes and experimental arenas of different shapes and sizes), followed individually during their lifetime (i.e. small colonies with short cycle), do not need intense care nor specific skills for maintenance (i.e. no beekeeping), and are relevant to address questions related to wild bee species (i.e. commercially available species are common in the wild). The ecological and economic importance of bumblebees, coupled with their global declines, has led to a significantly growing interest in their behaviour, ecology and evolution. In just about three decades, a generation of talented bumblebee researchers that have all marked their own fields (e.g. James Thomson: pollination ecology; Lars Chittka: behaviour and cognition; Juliet Osborne: foraging ecology; Paul Schmid-Hempel and Mark Brown: host-parasite interactions; Dave Goulson: pollinator conservation; Bernt Heinrich: energetics; Sydney Cameron: phylogeny; Sarah Alexandra Corbet: pollination ecology) have raised bumblebees at the level of model organisms for many areas of apidology and inspired many students now running bumblebee labs worldwide. This trend is illustrated by the sharp increase of published studies using bumblebees between 1990 and 2020, in research databases and the journal *Apidologie* (Figure 1).

In this short review, motivated by the 50th anniversary of *Apidologie* in 2020, we consider the growing importance of bumblebees for bee research, reflecting on its continued relevance. We explain how experimental studies became possible with the domestication and commercialization of bumblebees for crop pollination. We then describe how studies on bumblebees enabled major breakthroughs in comparative cognition, movement ecology, nutritional ecology, pollinator declines or evolutionary parasitology. We finally discuss some directions for future research in apidology and beyond.

2. THE RISE OF EXPERIMENTAL RESEARCH ON BUMBLEBEES

Bumblebees have long been recognised for their value as pollinators (Velthuis and van Doorn 2006). Because their proboscises are longer than those of honey bees (bumblebees: ca. 15 mm, honey bees: ca. 7 mm), bumblebees can pollinate flowers with deep corollas. This is why, for instance, they were imported to New Zealand at the end of the nineteenth century to improve the seed of a red clover used as forage for farm animals (Goulson 2010). At the beginning of the twentieth century, there have been many attempts by researchers to domesticate bumblebees from wild caught queens (Sladen 1912; Plath 1923; Frison 1927). Major steps included controlling climate (i.e. temperature and humidity) in rearing rooms, storing hibernating queens, breaking the diapause, controlling mating, and delivering appropriate pollen sources (Velthuis and van Doorn 2006). But it was not until the 1980s that routine domestication became a fact, when de Jonghe discovered the value of bumblebees for buzz pollination of tomatoes. Until then, tomato flowers in greenhouses were pollinated mechanically by vibrating the plants three times a week. In 1987, the first company for commercial rearing of bumblebees was created in Northern Europe. Today, the largest of these companies have rearing facilities all over the world. They mainly rear colonies for the local market using native species, so that five main bumblebee species are used for crop pollination (*Bombus terrestris* Linnaeus, 1758; *B. lucorum* Krüger, 1951; *B. occidentalis* Greene, 1858*; B. ignitus* Smith, 1869 and *B. impatiens*, Cresson 1863*)* (Velthuis and van Doorn 2006).

Commercial domestication dramatically boosted experimental research with bumblebees (Figure 1). Even though research had been conducted since the beginning of the twentieth century, most studies were published between 1975 and 2024. 88% of these studies were published after 1993, i.e. which was the first year when publications on bumblebees accounted for more than 15% of all publications on bees (Figure 1a). As a result of this sharp and continuous increase, 11,591 bumblebee studies were published as of 2024. This is one fifth of those published on honey bees, and more than those on solitary and stingless bees altogether. The same trend can be observed when considering only the publications in the journal *Apidologie* (Figure 1B).

3. MAJOR BREAKTHROUGHS INVOLVING BUMBLEBEES

There is now a rich history of bumblebee research with many influential labs across the world. *B. terrestris* is the main model species used by researchers based in Europe, while *B. impatiens* is used in North America, and *B. ignitus* in Asia. Often, the results described in one of these species were later confirmed in the others. Below we describe some research areas for which the utilisation of bumblebees sourced in the field or from commercial suppliers enabled breakthroughs in bee science and beyond (see summary in Table 1).

3.1. Cognition

Insect cognition research is living a golden age, with an increasing number of recent studies showing how insects solve ever more impressive problems despite their miniature brains (Chittka 2022). In this context, bumblebees have emerged as key models to experimentally explore the frontiers of insect cognitive capacities. These large and robust bees offer a unique opportunity to test individually identified insects in tightly controlled lab conditions. Foragers can be trained to collect nectar rewards over repeated trials in various kinds of mazes and arenas connected to their colony nest box, facilitating the implementation of protocols derived from experimental psychology used for testing humans or larger-brained vertebrates (see Figure 2). Over the past 20 years, this approach has been particularly fruitful, revealing an impressive behavioural and cognitive repertoire, that includes personalities (Chittka et al. 2003), numerosity (MaBouDi et al. 2017), social learning (Loukola et al. 2017; Bridges et al. 2024) (Figure 2b), emotional states (Perry et al. 2016), object categorization (Solvi et al. 2020) (Figure 2c), and path planning (Lihoreau et al. 2012b) (Figure 2d), to cite some. Most of these studies were based on the use of visual information, the neural processing of which is beginning to be understood thanks to anatomical and physiological studies of brain visual circuits (e.g. Sayre al. 2021).

3.1.1. *Social learning and cultural transmission*

Bumblebees have been central for the demonstration that insects can learn behaviours through the observation of others, an ability long been thought to be specific to vertebrates. In 2005, Worden (2005) and Leadbeater and Chittka (2005) used bumblebee colonies connected to lab arenas containing artificial flowers to show that inexperienced observers (i.e. bumblebees with no information on their foraging environment) can acquire flower preferences by looking at experienced demonstrators (bumblebees trained to visit flowers of specific colours). Social learning of flower preferences also works with resin bees placed on flowers instead of live demonstrators (Leadbeater and Chittka 2007). This ability is supported by associative learning (Dawson et al. 2013), allowing bumblebees to adjust their reliance on social information based on the context. Hence, social learning is more frequent when competition is low and the presence of other bees on flowers actually predicts a reward (Dunlap et al. 2016). Similarly, bumblebees can learn by observing foragers of other bee species that exploit the same resources, such as for instance honey bees (Dawson and Chittka 2012).

These findings raised the intriguing question of longer-term cultural transmission. Bumblebees were shown to be able to socially learn unnatural foraging tasks, including pulling a string with their mandibles to access an artificial flower (Alem et al. 2016; Figure 2a), rolling a ball to a specific location in order to be rewarded (Loukola et al. 2017; Figure 2b), and pushing coloured doors on puzzle boxes (Bridges et al. 2023). Remarkably, the individuals who observed a demonstrator pulling strings could not only acquire the novel behaviour of string pulling, but could then become demonstrators themselves, thus propagating these behaviours throughout the population (Alem et al. 2016), as later supported in other species (Danchin et al. 2018). More recently still, using a two-steps puzzle box, the same authors were able to show that bumblebees have the capacity to learn behaviours too complex for

Table I Some breakthroughs made possible through experiments with bumblebees. In this non-extensive list, we cite key references and associated species

Finding	Advantage of using bumblebees	Bumblebee species	Key references
Bees can learn new foraging techniques by observation of others (Figure 2a, b)	Bumblebees can be kept in colonies and trained to forage in artificial setups in the lab. Colonies are small; thus the experience of every individual can be monitored during its entire life	*B. terrestris*	Alem et al. 2016, Loukola et al. 2017 Bridges et al. 2024
Bees exhibit emotion-like states	Bumblebees can be kept in colonies and trained to forage in artificial setups in the lab	*B. terrestris*	Perry et al. 2016
Bees can consider their own body size to decide to move through a gap	Bumblebees can be kept in colonies and trained to forage in artificial setups in the lab. Colonies are small; thus the experience of every individual can be monitored during its entire life	*B. terrestris*	Ravi et al. 2020
Bees regulate their intake of protein, carbohydrates and lipids in food	Bumblebees can be kept in artificial colonies of controlled composition (e.g. with set numbers of workers and/or brood), and fed artificial diets in the lab	*B. impatiens* *B. terrestris*	Vaudo et al. 2016 Ruedenauer et al. 2020
Sublethal doses of pesticides affect many aspects of bee behaviour and social organisation	Bumblebee colonies can be kept and monitored in the lab. Colonies are small; thus every social interaction can be monitored	*B. terrestris* *B. impatiens*	Gill et al. 2012 Crall et al. 2018
Bees develop optimal multi-destination routes (Figure 2d)	Commercial colonies can be setup in the field. Bumblebees do not communicate locational information about food resources to nestmates. The colonies are small; thus every foraging event of an individual can be monitored	*B. impatiens* *B. terrestris*	Ohashi et al. 2007 Lihoreau et al. 2012b
Bees display sophisticated flight control (Figure 2e)	Freely moving bumblebees can be trained to forage in virtual reality flight arenas in the lab	*B. ignitus*	Frasnelli et al. 2018
Immune responses incur important fitness costs	Bumblebees are robust to injections and manipulations. They can be kept and monitored in isolation in the lab for weeks	*B. terrestris*	Moret and Schmid-Hempel 2000
Polyandry benefits to prevent infections	The reproduction of bumblebees can be manipulated. They are easily infected in the lab	*B. terrestris*	Baer and Schmid-Hempel 1999

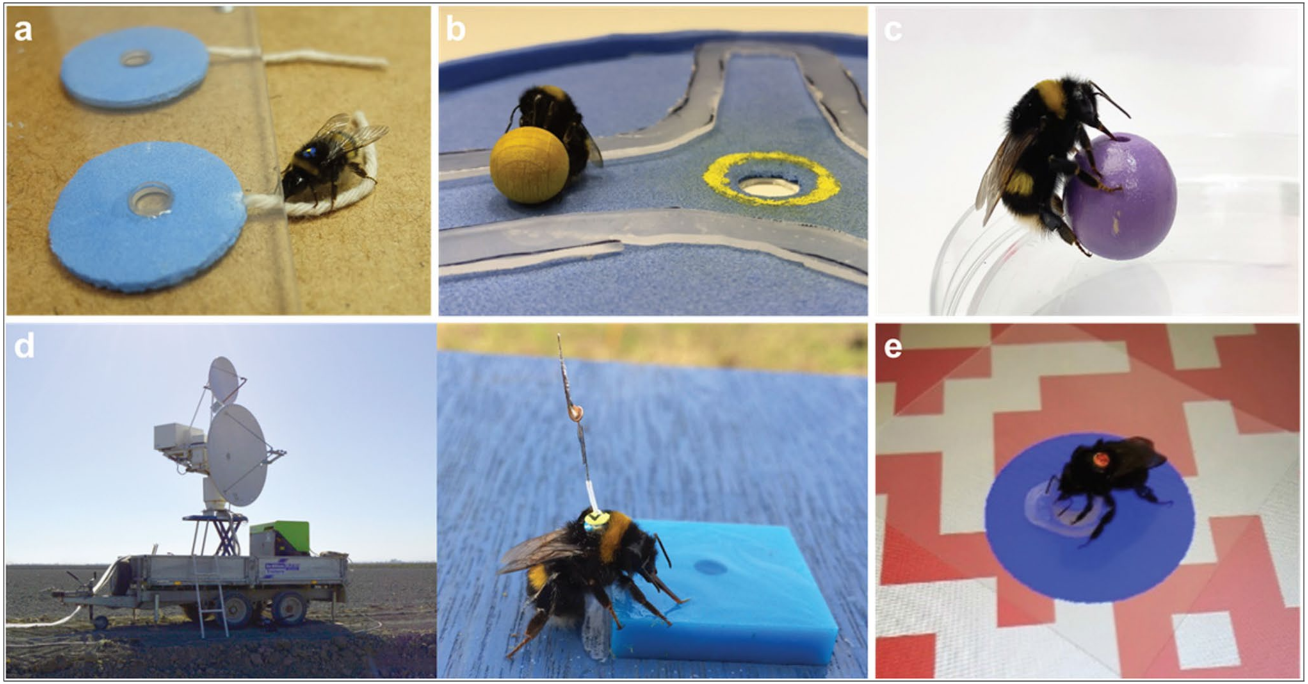

Figure 2. Bumblebees are particularly suitable for experimental research. (a) Setup used by Alem et al. (2016) or observational learning of foraging techniques**.** The bumblebee is pulling a string to move a feeder containing a reward. Photo provided by Olli Loukola. (b) Setup used by Loukola et al. (2017) to demonstrate innovation. The bumblebee is moving a ball to the center of a feeder**.** Photo provided by Lars Chittka (c) Setup used by Solvi et al. (2020) to test the ability to discriminate geometric shapes visually or by touch. The bumblebee is getting a reward from a spherical object. Photo provided by Cwyn Solvi. (d) Harmonic radar used by Lihoreau et al. (2012a, b) to demonstrate route optimisation (left) and transponder used to track bumblebees (right). Photos provided by Tamara Gómez-Moracho (radar) and Joe Woodgate (bumblebee on feeder). (e) Virtual reality setup used by Frasnelli et al. (2018) to show the role of visual motion cues in navigation. The bumblebee is getting a sucrose reward from a virtual feeder displayed on a LCD monitor on the ground. Photo provided by Elisa Frasnelli.

any individual to innovate alone (Bridges et al. 2024), a skill necessary for cumulative culture which has never before been convincingly shown in a non-human animal. These remarkable abilities may explain the frequent emergence of cheating behaviours in natural bumblebee populations, where foragers bite holes into the base of flowers to facilitate nectar collection instead of landing or entering the flowers (Leadbeater and Chittka 2008). As bumblebee colonies only survive for one season, it is no surprise that we have yet to find natural innovations that persist over several years, however the fact that the capacity exists opens some exciting questions for social insects as a whole.

3.1.2. *Emotions and pain*

Bumblebee research is central to recent debates around questions of invertebrate welfare, such as the question of emotions and emotion-like states, pain and suffering, and sentience. In questioning the capacity for emotion, one well-established method to approach this question is through the use of cognitive bias tests, where the subject is trained to two stimuli (one rewarded, the other punished) then presented with an ambiguous version of the same stimulus. Perry et al. (2016) were able to show instead that bumblebees exhibited a positive bias in response to an ambiguous stimulus after the bee had received an unexpected reward. Indeed, after receiving this unexpected reward, bumblebees were quicker to approach an ambiguous stimulus than unrewarded conspecifics. These ‘optimistic’ bumblebees were quicker to resume their activity after a simulated predator attack (squeezed by a sponge) and the effects were abolished with topical application of a dopamine antagonist, suggesting common neural processing features to that of vertebrates (Perry et al. 2016).

Perhaps more closely linked to questions of welfare is the debate around pain and sentience in invertebrates, especially while insect farming is gaining in popularity. Separating the experience of pain from a simpler mechanism to avoid noxious stimuli is of course not possible without self-report. Bumblebees were however shown to be able to modulate their response to a noxious stimulus — in this case balancing the value of different rewards with the negative experience of a heated surface (Gibbons et al. 2022). Here, sugar water was available on two artificial flowers, the base of which could be heated to high temperatures, something bumblebees normally show strong avoidance to. As expected, bumblebees would avoid the heat pad when it led to low quality sugar reward, but remarkably they would voluntarily experience this heat for short intervals if it led them instead to a high-quality reward. This suggests at least a more complex valuation of noxious stimuli than the expected reflexive avoidance.

3.1.3. *Internal representations of the world*

Another important effort of bumblebee research is being made to understand how information is processed and stored in the insect brain. This includes how reward attributes are valued (i.e. comparisons; time-delays), and how this affects subsequent behaviour (i.e. reward-modulated attention). It also includes how insects may perceive themselves and their own ability. For instance, Ravi et al. (2020) showed that flying bumblebees judge whether they can move through a gap based on knowledge of their body size. The authors trained small and large bumblebees to fly through a wall with a hole leading to a foraging arena. Using high-speed 3D video tracking, they found that bees successfully flew through narrow gaps, even those that were much smaller than their wingspans, by first performing lateral scanning to visually assess the aperture, and then reorienting themselves, sometimes flying sideways. This suggests that insects account for their own size and shape to safely navigate through complex environments.

As well as their own size and shape, animals may need to develop internal images of their world and transfer these images across sensory modalities so the information can be used in different contexts. For instance, we humans build mental images allowing us to recognize an object out of view, only by touch. Solvi et al. (2020) tested this ability in bumblebees searching for sucrose rewards in objects distributed in a lab flight arena, either visually or by touch (Figure 2c). Bumblebees trained to discriminate cubic against spherical objects using vision behind a screen, could apparently also recognize by touch only in the dark, and vice versa. This suggests that insects form modality-independent internal representations of object shapes, an ability that we humans are explicitly self-aware of, although other explanations cannot completely be ruled out for insects (Le Moël et al. 2020).

3.2. Navigation

Studying bee movements across landscapes is a longstanding challenge, key to understanding how insects perceive the world and pollinate plants. Since Karl von Frisch (1967) cracked the code of the honey bee waggle, most research on bee navigation and large-scale foraging has focused on how individual foragers learn to move between its colony nest and one or two feeders. Reading the waggle dance can tell researchers how distances and directions to the feeders are perceived, learnt and communicated by the bee. This has been particularly useful to understand the basic 'tool box' underpinning bee navigation (e.g. path integration (Srinivasan et al. 2000)) and explore the ways in which space could be encoded in a miniature brain (Cheeseman et al. 2014; Hadjitofi and Webb 2024). However, the more recent utilisation of bumblebees in navigation studies considerably broadened the scope of investigations, with new emerging scientific questions. Unlike honey bees, bumblebees do not communicate the location of food resources to their nestmates (Dornhaus and Chittka 1999). This means foragers must search and exploit for multiple food resources by themselves, based on their own experience. Accordingly, the focus of bee navigation research has tended to shift from single-destination to multiple-destination route learning. This change was facilitated by the fact that bumblebees live in small colonies in which every individual can be distinctively tagged and tracked during their entire lifespan (Woodgate et al. 2016).

How multi-destination routes develop is a key example. For bee species exploiting patchily distributed resources, visiting multiple feedings sites in an efficient way represents a challenging routing problem (Lihoreau et al. 2013). Bumblebees, and many other wild bees, have long been reported to visit familiar feeding sites in a stable order, a routing behaviour called 'traplining' (Thomson et al. 1997). Using semi-automated feeders to remotely replenish feeding sites, it was shown that individual bumblebees spontaneously learn and remember efficient (if not the shortest possible) traplines to visit all feeders once and bring back food to their colony nest (Ohashi et al. 2007; Lihoreau et al. 2012a). This behaviour was observed in arrays of feeders with various geometries and at different spatial scales in the lab and in the field. Detailed monitoring of bumblebee flight paths with harmonic radar in commercial colonies placed in the field (Figure 2d), revealed foragers reduced overall travel distance using flight vectors to link flowers following the shortest route, while maintaining high levels of exploration to react to potential changes in resource availability (Lihoreau et al. 2012b; Woodgate et al. 2017). Recently, honey bees were also shown to learn near optimal routes between a small number of feeders (although less efficiently), suggesting that this spatial behaviour is shared by many bee species (Buatois et al. 2024).

3.3. Nutrition

Bees have been central for the development of optimal foraging theory in the 1970s (Charnov 1976), assuming that they prioritised visits to flowers delivering nectars with the highest concentrations of carbohydrates or in the largest volumes (e.g. Pyke 1980). In recent years, however, advances in nutrition research have revolutionised this vision, demonstrating the need for foragers to collect different nutrients in specific amounts and balances, in order to meet the diverging needs of all colony members, depending on their castes, developmental stages, and health status, as well as climatic conditions

(Wright et al. 2018). The picture is more complex than previously thought, and bumblebees have played an important role for unravelling these regulatory processes thanks to the possibility to maintain functional microcolonies foraging on artificial diets in the lab.

3.3.1. *Nutrient balancing*

The ability of bees to balance their diet has been demonstrated using nutritional geometry, a conceptual framework to study food choice and its fitness consequences (Raubenheimer and Simpson 2020). "Cafeteria" experiments, in which insects can select artificial diets of known nutritional compositions, are powerful means to identify nutritional needs and strategies employed to meet them (Lihoreau et al. 2018). With this approach, Stabler et al. (2015) demonstrated that bumblebee workers given access to liquid diets (artificial nectars) collected different volumes of the diets in order to reach a 1:149 w/w protein to carbohydrate ratio. This selective nutrient collection varies with the form of the nutrients in food (e.g. free amino acids or bounded in proteins) (Stabler et al. 2015). Studies using solid diets (artificial pollens) in food choices highlighted the importance of regulating lipid collection: as bumblebees avoid over ingesting fat contrary to protein and carbohydrates (Vaudo et al. 2016; Kraus et al. 2019). Lipid intake increases the performance on visual learning and survival (Muth et al. 2018) but can also be toxic when consumed in excess (Vaudo et al. 2016; Muth et al. 2018).

3.3.2. *Food quality perception*

Bumblebees have also been critical to understand nutrient sensing by pollinators. Bee foragers assess food quality using chemotactile and nutritional cues, such as nectar viscosity and sugar concentration (Zhou et al. 2024). Protein and lipids can also be sensed in pollen (Ruedenauer et al. 2020). For instance, bumblebees whose proboscis extension reflex was conditioned can predict the income of a reward by discriminating the presence of proteins in the conditional stimulus (Ruedenauer et al. 2015). While olfactory cues alone enable such detection, chemotactile cues through antennal contacts are necessary to sense the presence and concentration of proteins. All of these sources of information help bees to select the quantity and balance of nutrients needed. Note however that other food compounds can influence bee nutritional choices. In particular, foragers can be tricked by secondary metabolites such as caffeine and nicotine, that, even in low amounts, can attract bees to flowers with nectar and/or pollen of suboptimal nutritional contents (e.g. Baracchi et al. 2017).

3.4. Environmental stressors

Wild bees are declining in most of the industrialized world. This decline has received considerable attention in the past decade as the loss of main pollinators can have dramatic consequences on ecosystems and food security (Goulson et al. 2015). Bumblebees are increasingly used as sentinel species to assess environmental risks for pollinators and have been key to demonstrating the impact of agrochemicals on pollinators. Firstly, their small and manageable colonies offer a unique opportunity for a comprehensive assessment of the multi-level effects of controlled exposure to stressors on individuals and colonies. Secondly, in contrast to domesticated honey bees that are managed by humans throughout their development, results on commercial bumblebees can be more realistically extrapolated to natural populations and other declining wild bees, although population of domesticated bumblebees are not declining.

3.4.1. *Pesticides*

Neonicotinoid pesticides are arguably one of the main contributors to bee declines (Goulson et al. 2015). These are widespread insecticides sprayed on plants, applied to soils or used for seed coating of flowering crops for pest control.

While the first negative effects of an exposure to low concentrations of these compounds were reported on honey bees (Henry et al. 2012), detailed analyses of sublethal effects come from observations on bumblebees. For instance, Kessler et al. (2015) investigated whether bumblebees could detect neonicotinoids in food. Bumblebees exposed for 24 h to field-realistic concentrations of three main neonicotinoids (Imidacloprid, Thiamethoxam, Clothianidin) were unable to avoid natural concentrations and increased their food consumption, even though high concentrations significantly reduced their survival. Electrophysiological recordings of gustatory neurons located on the proboscis revealed that bees lack taste neurons responding to these compounds. In fact, bumblebees acquired a preference for treated food (presumably because they target neural circuits causing addiction) (Arce et al. 2018), increasing all the more the risks for the colony during prolonged pesticide exposure.

To mimic a realistic scenario of exposure and better assess the potential of colonies to buffer combinatorial effects, Gill et al. (2012) exposed bumblebee colonies to field-realistic concentrations of the neonicotinoid Imidacloprid, the pyrethroid Cyhalothrin and both. Chronic exposure to the two pesticides impaired natural foraging behaviour, significantly reduced brood development and colony success, highlighting that combined exposure to pesticides increases the propensity of colonies to fail. Crall et al. (2018) developed an automated robotic platform for continuous, multi-colony monitoring of uniquely identified workers in the long term, which would be hardly feasible with much larger honey bee colonies. They demonstrated that chronic exposure to field-realistic levels of Imidacloprid impaired the in-nest behaviour of workers, including nursing and social interactions. These results highlight the multifaceted behavioural impacts of neonicotinoids and illustrate the potential of high-throughput, automated analysis for improving the understanding of agrochemicals impacts (Marchal et al. 2019). Mechanistic approaches like brain cell cultures (Moffat et al. 2015), brain volumetrics (Smith et al. 2020), pharmacology and genomic studies have also started to reveal some details of the molecular and cellular actions of these molecules that may explain their behavioural consequences in bumblebees.

The detailed studies of the sublethal effects of harmful pesticides such as neonicotinoids resulted in a more constrained utilisation of these compounds. This legislative reassessment led to the development of alternative practices and products (Colin et al. 2020). Here again bumblebees have become tractable models for a rapid risk assessment through the screening of multiple behavioural traits across several colonies. For instance, Sulfoximine-based insecticides are a priority issue since they are the most likely successors of neonicotinoids (Brown et al. 2016), already licensed for use (China, USA) or under consideration (European Union). In an attempt to pre-emptively evaluate their potential sub-lethal effects on pollinators, Siviter et al. (2018) chronically exposed bumblebee colonies to Sulfoxalor at concentrations consistent with potential post-spray field exposure. They showed this new compound had severe sub-lethal effects on colony development. The difference between life-history trajectories of treated and control colonies appeared at the eclosion of larvae, suggesting potential cumulative long-term consequences for colony fitness. These results call for caution against the use of Sulfoximine as a direct replacement for neonicotinoids.

More recently, Nicholson et al. (2024) have used bumblebees to highlight weaknesses in current pesticide regulation, even in countries where neonicotinoids and sulfoximines are restricted. They analysed the impact of pesticide exposure on 316 bumbleblee colonies located near agriculture sites across eight European countries. Colony performance (colony weight and number of individuals) before and after cultural bloom was significantly reduced by the exposure to pesticides, with up to 27 compounds recorded in the pollen stores. These findings suggest that current pesticide regulation fails to properly protect pollinators effectively, highlighting the need for post-approval monitoring of pesticides to minimize environmental damage.

3.4.2. *Combinations of stressors*

The study of the impact of environmental stressors on pollinators calls for a holistic approach. But disentangling the individual and interacting effects of stressors, at different scales (individuals, colonies, populations), is a considerable challenge that cannot be done by empirically testing all combinations and contexts. Mechanistic models have been used to better explore the multilevel impacts of populations under stress. To answer this need for structural realism with the incorporation of multiple stressors operating at different organizational levels, Becher et al. (2018) developed the Bumble-BEEHAVE model. In this approach, and its subsequent derivations, simulations can predict the effects of multifactorial stressors on bumblebee survival at the individual, colony and population levels. One important aspect of modelling bumblebee colonies is the ease at which model predictions can be tested using toxicological experiments and measures of demographic traits on actual colonies in the lab or semi-field conditions (Gill et al. 2012; Crall et al. 2018). This represents a significant step towards realistically predicting bee population dynamics under stress. It can be used by scientists and stakeholders, for instance, to explore combined effects of stressors on population success, to predict pollination services, to test the relative effects of policy recommendations, all in realistic landscapes.

3.5. Host-parasite interactions

Bees are hosts of a large number of parasites and pathogens including viruses, bacteria, fungi, protozoa, nematodes as well as other arthropods (i.e. diptera parasitoids, acarids) (Schmid-Hempel 2001). Commercial bumblebees provide many advantages to study these host-parasite interactions. Firstly, individuals of all developmental stages (larvae, adults) can be exposed and maintained in the lab, thus allowing for precise and differentiated manipulations of host-parasite interactions. Secondly, colony members are full siblings (most bumblebee species are monandrous (Estoup et al. 1995)), thereby providing optimal conditions for parasite transmission across nestmates (Baer and Schmid-Hempel 2003). Indeed, genetic diversity is thought to reduce parasite infection in insect colonies, as shown in *B. terrestris* gynes artificially mated with multiple males that produced colonies with better reproductive success and lower parasite prevalence than colonies from monandrous queens (Baer and Schmid-Hempel 1999).

3.5.1. *Transmission dynamics*

Among the numerous parasites of bumblebees, the trypanosome *Crithidia bombi* has received the most attention, both because it is highly prevalent in the field (e.g. up to 82% in North America (Gillespie 2010)) and can lead to colony collapse (Schmid-Hempel 2001). *C. bombi* is a gut parasite that is transmitted horizontally within colonies by ingestion of parasite cells in contaminated faeces (Solter et al. 2012). Using automated video-tracking to record the movements of every worker in colonies, Otterstatter and Thomson (2007) showed that infection spreads more or less rapidly depending on the density of individuals and the properties of contact networks. Durrer and Schmid-Hempel (1994) further showed that horizontal transmission is common between colonies and between species exploiting common resources. The probability of transmission depends on the body size and activity of the foragers, as well as floral traits, such as corolla size (van Wick et al. 2022).

3.5.2. *Immune responses*

Once parasites or pathogens enter the host, an immune response is activated. Bumblebees have recently emerged as a model system to study collective and individual immunity in social insects. At the colony level, bumblebees display cooperative behaviours to prevent and fight infections (i.e. social immunity). For instance, workers parasitized by conopid flies tend to spend nights outside the nest, which delays the development of the parasites due to lower temperatures (Müller and Schmid-Hempel 1993). At the individual level, it is possible to study the immune response of bumblebees by evoking parasite infection with injection of immune elicitors such as lipopolysaccharides (LPS) or sterile micro-latex beads (Moret and Schmid-Hempel 2000). For instance, the injection of LPS decreases the production of an immune response which reduces the survival (Moret and Schmid-Hempel 2000) and the foraging efficiency (Mobley and Gegear 2018) of individuals. Further studies showed that individual immune responses are context-dependent, modulated by the social environment. Accordingly, bumblebee workers maintained in groups exhibited an enhanced expression of antimicrobial peptides (AMPs), compared to conspecifics kept in isolation that, by contrast, showed a higher phenoloxidase activity (Richter et al. 2012). The immune response can also be transmitted to the next generation, even though insects do not produce antibodies that could transmit specific immunity (Sadd and Schmid Hempel 2007). Indeed, bumblebee colonies challenged with LPS produced males with increased constitutive immunity, displaying high phenol oxidase (PO) activity, a protective factor against microorganisms (Moret and Schmid-Hempel 2001). Triggering the immune response with LPS can prove very useful to disentangle the consequences of parasite infection or the immune response itself. Additional factors can also affect bees' susceptibility to infections. Heatwaves, for instance, considerably comprises the immune response of bumblebees infected by *C. bombi* (Tobin et al. 2024).

3.5.3. *Self-medication*

Studies using bumblebees revealed the existence of antiparasitic nutritional behaviour by which infected individuals consume anti-parasitic substances, such as many secondary metabolites found in nectar or pollen. In particular, the consumption of alkaloids by bumblebees can significantly reduce individual infections by *C. bombi* and *Nosema bombi* (Richardson et al. 2015, Manson et al. 2010), and therefore the prevalence of parasites in colonies (Folly et al. 2021). Using artificial flowers, infected bumblebees have been observed to actively seek for antiparasitic diets containing nicotine, ultimately slowing down the progression of *C. bombi* infection (Baracchi et al. 2015). Such modification in the diet of parasitised animals, towards a harmful compound for healthy individuals, is consistent with a self-medication strategy.

3.5.4. *Microbiota*

The host microbiota of insects can also be involved in defence against parasites (Koch and Schmid-Hempel 2011). This is the case of the community of bacteria inhabiting the bumblebee gut, which is mainly composed of Gammaproteobacteria, Firmicutes, Betaproteobacteria and Alphaproteobacteria (Koch and Schmid-Hempel 2012). Bumblebees raised in social isolation and later fed faeces from nestmates developed a similar microbiota community as their conspecifics, which confers them protection against *C. bombi*, as measured by lower parasite loads than workers fed antibiotics or other bacteria (Koch and Schmid-Hempel 2011). Beyond this antiparasitic effect, the microbiota can mediate entire host-parasite interactions. By swapping the microbiota between bumblebees from different colonies and infecting them with different *C. bombi* strains, Koch and Smith-Hempel (2012) showed that the microbiota was driving host-parasite interactions more than host genotype and that some specific strains of *C. bombi* were more successful to develop and generate infection with different microbiota patterns. Gut transplants experiments from donor bees also enables to explore the interaction between gut microbiome and diet on the susceptibility to parasite infections. For instance, gut transplants from bees fed pollen that have been associated to lower parasite loads (i.e. sunflower) help to elucidate the effect of pollen itself or subsequent changes in the microbiome on parasite infection (Yost et al. 2023).

3.5.5. *Behavioural effects*

Parasites and pathogens often influence the behaviour of their hosts, and sometimes even manipulate them to enhance their own chance of reproduction and dispersion (Ponton et al. 2006). Bumblebees have been important to clarify some effects of common parasites on wild bees in laboratory setups. For example, bumblebees exposed to *Nosema ceranae* in food, a microsporidian parasite of honey bees (Higes et al. 2006), showed reduced olfactory learning (Gomez-Moracho et al. 2022). Bumblebees infected with *C. bombi* showed reduced abilities to learn to discriminate flowers of different colours and odours (Gegear et al. 2006). These cognitive impairments are likely due to the induced immune response rather than to the action of the parasite itself, since bumblebees injected with LPS show similar troubles when learning colours of rewarding flowers (Alghamdi et al. 2008).

4. PERSPECTIVES

Over the past decades, bumblebees have emerged as model species to study various aspects of apidology, sometimes opening up the possibility to tackle problems with new angles as compared to more classical bee models such as honey bees. This is because bumblebees can be handled in the lab all year round, and allow easier experimental manipulation of their small-size colonies. Importantly, many of the findings on bumblebees have been later confirmed in honey bees but also in other wild bee species, demonstrating their utility as model species (e.g. Riveros and Gronenberg 2009; Buatois et al. 2024). As a result, experimental research on bumblebees is developing quickly and yields considerable promises for future research on emerging topics on bee behaviour and ecology. Below we list some of these exciting avenues.

Bumblebees have been used in highly artificial experimental setups to study fundamental principles of vision underpinning various forms of learning, memory and navigation (Figure 2). Several new insights may arise from fast developing technologies to test and track insects. For instance, studies have begun to develop virtual reality setups in which freely moving individuals can be trained to fly and forage in virtual worlds and return to their colony (Frasnelli et al. 2018) (Figure 2e). Using virtual worlds enables a precise control of the visual stimuli available to insects. It therefore brings new avenues to study how flying insects learn different types of visual cues and selectively use them in different contexts of navigation, such as search, homing or route development. Virtual reality could be used for controlling the visual experience of the bee during training and implementing typical displacement experiments (i.e. the bee is caught at a familiar site and released at an unfamiliar site). In this approach, potential biases resulting from uncontrolled familiarity of bees with their visual environment would be totally precluded, a prerequisite for further exploration of the internal representation of space in the bee brain (Cheung et al. 2014).

Bumblebees are large and robust insects that greatly facilitate the study of spatial movements in the field. They can carry tags or transponders often required for automated movement tracking using radars (Riley et al. 1996) or telemetry (Daniel Kissling et al. 2014). Developments of such tracking technologies are necessary to study how bees navigate and interact over large spatial scales (beyond the ca. 1-km catchment area currently possible with a harmonic radar), and in three dimensions (for instance between resources at ground level and on top of hills), which may require even larger equipment. Bumblebees are particularly suitable for research on social and competitive interactions as they do not exploit resources en masse, thus enabling addressing questions about resource partitioning that may face most pollinators (Pasquaretta et al. 2019). All these aspects of bee navigation are still poorly understood but may be most easily addressed with bumblebees.

Automated monitoring systems based on computer vision now allow to track in real time the behaviour of all individuals simultaneously with unprecedented details, both in and out of the hive (Marchal et al. 2019). Bumblebees greatly facilitate these approaches due to their relatively small colonies in which all individuals can be tagged for individual identification. As illustrated above, such detailed analyses of bee behaviour and interactions can inform about stress levels (Gill et al. 2012; Crall et al. 2018). Further developments of these methods will allow to better capture the sublethal effects of environmental stressors — including new molecules to be put on the market — by considering a wider diversity of fitness-related traits than the classical survival or more recent cognitive deficits. In particular, the detailed understanding of the nutritional requirements of bumblebees and their responses to environmental changes may offer powerful ways to mitigate these non-desired effects. It is easy to envision how this knowledge can be used for conservation, by offering plants with pollen and nectars providing the required nutrients for colony development and reproduction (Vaudo et al. 2020). A similar approach could be used to maximise the efficiency of plant pollination by commercial colonies, for instance by attracting bees on specific plant resources that will meet the specific nutritional needs of colonies.

The utilisation of bumblebees holds considerable promises for developing mechanistic studies thanks to the development of biotechnologies to study brains and the neuro-genetic bases of behaviour. A promising avenue is the opportunity to characterize behavioural intra- and inter-individual variability and understand their neural bases. For this, the influence of body size in division of labour (rather than age as in honey bees) offers an interesting model for studies of plastic behaviours. Indeed, for bumblebees the probability to engage into foraging tasks increases with body size, which is easily measured and varies greatly within colonies (Brian 1952). Although brain size correlates with body size, some brain centres likely involved in important cognitive functions (e.g. navigation, learning) show allometric relationships (Mares et al. 2005). In addition, their maturation appears to be partially shaped by life experiences such as early sensory stimulations (Jones et al. 2013) and foraging experience (Riveros and Gronenberg 2010). Thus, the emergence of at least some of the remarkable behaviours described in this review may depend on specific developmental trajectories and/or life histories, and may contribute to a loose but efficient task specialization within small colonies.

Finally, it is very likely that bumblebees become genetic models in the near-future. Current attempts to edit genomes of honey bees with the CRISPR/Cas9 tool face the difficulty of creating and maintaining genetic strains (queens must be genetically modified, and long-lived colonies — strains — must be maintained) (Otte et al. 2018). This also raises the problem of unwanted gene flows if genetically modified gynes or males escape in the wild. As the genome of some bumblebee species is now available (Sadd et al. 2015), bumblebees constitute attractive organisms for genetic manipulations, with their short colony cycles, and the possibility to confine colonies more easily in the lab.

5. CONCLUSIONS

Bee research has long focused on honey bees for practical reasons and because they display a fascinating social life. However, just like for all other disciplines of biology and ecology, moving away from research based on single model organisms, by adapting the choice of species to the addressed scientific questions is a good thing that may open new opportunities and lead to breakthroughs (Laurent 2020). As we have seen above, bumblebees offer many opportunities for studying new aspects of bee behaviour in laboratory setups but also in the wild. Since their domestication for commercial pollination, bumblebees have constituted tractable species to work with and address questions that are difficult to tackle with honey bees or some other domesticated bees. However, raising bumblebees at the level of model species has also some drawbacks, one of which is the loss of diversity in populations and species studied. The focus on a few commercially available species has led to an erosion of skills and has diminished interest in several lines of research as for intra and interspecific comparisons that was high before commercial domestication (e.g. Laverty and

Plowright 1988). Although an important advantage of using bumblebees is the relevance of the results for wild pollinators, differences in behaviour and stress tolerance between domesticated and wild bumblebees should be studied in more details. Ultimately increasing the diversity of species in bee research, in particular those topics related to pollination and conservation, can only be beneficial to identify suitable solutions against population declines, as these species are likely to have different nutritional requirements and responses to stressors. Bumblebee researcher should consider re-engage in lab-rearing colonies in order to reactivate these important lines of research for our understanding on bee ecology and evolution.

ACKNOWLEDGEMENTS

The authors thank Jean-Marc Devaud, Alexandre Dore, Thibault Dubois, Ana Moran-Hernandez, Stéphane Kraus for discussions on a previous version of this manuscript.

AUTHOR CONTRIBUTIONS

MLi wrote the first draft. All other authors contributed significantly to revisions.

FUNDING

Open access funding provided by Université Toulouse III - Paul Sabatier. This work was funded by the ERC Consolidator grant Bee-Move (GA101002644) to ML.

DATA AVAILABILITY

N/A

CODE AVAILABILITY

N/A

DECLARATIONS

Ethical approval N/A

Consent for publication N/A

Consent to participate N/A

Conflict of interests The authors declare no conflict of interest.

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