Bumblebees as a powerful model for the study of cognitive ecology

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Abstract

Bumblebees have been used to study various aspects of complex cognition and behavior, yet unlike many purely lab-based systems, we also possess rich knowledge of their natural history. We highlight how integrating these perspectives has provided insights into both the underlying mechanisms and functions of cognitive abilities.

Comparative cognition seeks to understand whether superficially similar behaviors across species are underpinned by shared or distinct cognitive mechanisms. In general, the anthropocentric perspective focuses on whether a non-human animal *can* do something, based on human-defined cognitive complexity. In contrast, the ecological perspective focuses on *why* animals behave the way they do, considering cognition in the context of the species' ecology and evolution. We highlight how research in bumblebee cognition has allowed researchers to integrate these perspectives to interpret behavior, make cross-species comparisons, and address evolutionary questions. We focus on bumblebees because they have emerged as a powerful invertebrate model in the study of cognition, demonstrating abilities once thought to be unique to vertebrates and raising questions about the evolutionary origins and taxonomic prevalence of these abilities.

Why bumblebees?

One of the key advantages of studying bumblebees comes from their experimental tractability: hundreds (or more) of individual bumblebees can readily be studied in a lab set-up, a semi-field environment (e.g., where colonies are maintained and monitored in a lab, but bees can forage outside), or in the wild. These features have allowed researchers to explore a broad variety of topics in cognition that are more difficult to study in larger, longer-lived species. Another key strength comes from bumblebees' motivation to engage with a wide array of experimental stimuli and tasks, allowing for a range of questions and comparison with other species presented with similar tasks. This motivation and skill come from bumblebees' natural behavior as generalist foragers, which involves visiting a wide variety of flowers that vary in both their sensory stimuli and the motor routines needed to access their rewards (Fig. 1, Box 1). While many model species are studied in contexts divorced from their natural ecology, for over a century, bumblebee ecologists have assembled a tremendous wealth of natural history knowledge through observation and experimentation [1], allowing bee cognition to be understood in its ecological and evolutionary context.

Using bumblebees to reveal cognitive mechanisms behind behavior

Determining the cognitive mechanisms behind behavior is essential to understanding how behavior is generated and for making informed cross-species comparisons, since similar behaviors can be driven by distinct mechanisms. For example, bumblebees show the capacity for numerical cognition, considered a hallmark of 'complex cognition' [2]. However, rather than solving numerosity tasks in a manner akin to mammals (i.e., sensing number in a rapid 'snapshot' or 'subitizing'), bumblebees sequentially scan patterns to enumerate the countable elements within a pattern [2]. This finding was revealed through detailed flight-path analysis of bees visiting artificial flowers containing different numbers of pattern elements and showing that the bees inspect pattern elements up close and one by one [2]. This strategy likely comes from the fine-scale pattern recognition bumblebees use to distinguish between flowers (e.g., Fig. 1A). Indeed, a subsequent study demonstrated via a neural network model that a simple scanning strategy, such as measuring the transitions from dark regions to light regions, can explain bee 'counting' behavior [3]. Thus, a behavior that on the surface appears akin to that of mammals, is underpinned by different mechanisms, which may have different implications for the contexts to which it extends; for example, bees may not be able to 'count' higher numbers or form numerical concepts more broadly [3], but may be particularly adept at recognizing subtle differences in visual patterns. Similar approaches have revealed how sophisticated pattern recognition and concept learning in bees can be explained through their visual ecology and search behavior [4].

Using bumblebees to place cognitive mechanisms in an evolutionary context

Along with determining cognitive mechanisms underpinning behavior, an appreciation of ecology can place those mechanisms in context, allowing broader inferences about the evolution of cognitive abilities. One compelling example of this comes from work on bumblebee social learning. Across many types of complex behavior, bumblebees consistently learn the task using associative rules. An elegant study showed that their social learning, too, can be underpinned by associative learning, specifically second-order conditioning [5]. Bumblebees have also demonstrated 'behavioral traditions' in a lab context [6], where a socially learned behavior spreads throughout the group and is maintained over time; and similar mechanisms also likely underpin this behavior (as discussed in [5], [6]). Knowledge of bumblebee natural history allows these findings to be placed in context: while bumblebees are capable of behavioral traditions in an experiment, it is unlikely that behavioral traditions exist in the wild because generations are generally non-overlapping (except for in some temperate regions). Yet the finding that bumblebees *can* socially learn and form behavioral traditions shows that the ability to associatively learn a broad variety of stimuli may be sufficient for this behavior to arise. Therefore, while this does not necessitate that all animals with behavioral traditions or culture are implementing the same cognitive mechanisms as bees, it indicates that the limited examples of culture in non-human animals may be due to a lack of appropriate conditions, rather than rare cognitive abilities.

Understanding the evolution of cognition through bumblebee-plant interactions

Finally, researchers have demonstrated how bee cognition and foraging environments influence each other at an ultimate level. For instance, bees' cognition shapes their environments via selection on traits of the flowers they pollinate. A series of experiments has shown that bumblebees shape floral traits of *Brassica rapa* within just a few generations. In one study, plants pollinated by bumblebees evolved to be taller and have more fragrant flowers with increased UV reflection [7], in line with what is typical for bee-pollinated (or 'bee-syndrome') flowers. More recent work is now building upon these studies to delve into the genomic mechanisms underpinning such changes, as well as how selective pressures from pollinators intersect with those from herbivores and other floral visitors. Bee-visited plants, in turn, can also select for particular cognitive abilities – and this research can reveal vital information about the evolution of cognitive traits more broadly. For example, a recent study highlighted how the benefits of cognitive performance can be context-specific. While it is often implicitly or explicitly assumed that better performance at a cognitive ability correlates with a fitness outcome, field-based work shows that the relationship between cognition and fitness is often not as predicted (reviewed in [8]). In bumblebees, a fascinating example shows that working memory predicts foraging success (a fitness proxy) in the spring but not the summer [12]. This may be explained by the fact that in the environment in which bees were tested, floral resources were more plentiful and diverse in the spring compared to the summer [9]. Beyond bees, these results demonstrate that selection pressures on cognition can stem not only from harsh environments but also from having to cope with the richness of an environment.

The future of bee cognition

Despite the many lessons already learned from bumblebees, this system continues to hold tremendous potential for asking broad, ecologically informed questions going forward. For example, the incorporation of ecologically relevant features into experimental paradigms has long allowed researchers to probe the limits of bee cognition, and incorporating more naturalistic features could yield further insights (Box 1; see also [10]). In addition, the majority of work in bumblebees has focused on two commercially-available species (*B. impatiens* and *B. terrestris*) and the foraging worker stage, with much less known about the ~250 species worldwide and the other workers and castes. Bumblebee queens also forage at a solitary stage while nest-searching and are better at learning associations than workers [11]. This suggests particularly strong selective pressures to learn at this stage, and hints at the possibility of other cognitive differences between castes reflective of differences in their environments, yet this remains unknown – and as described above, the relationship between cognition and fitness is not straightforward.

Beyond bumblebees, there are ~20,000 other bee species with varied natural histories, offering a tremendous untapped pool in which to ask broad questions about how environments can drive the evolution of specific cognitive abilities. While there are logistical challenges involved in working with understudied species, many of these species are already being studied in other areas of biology, such that cognition researchers may benefit from the natural history knowledge already gained through interdisciplinary collaboration. While wild bees carry the limitation of not knowing their past experiences (which likely influence cognitive performance), this, alongside the greater genetic variation, may be an important aspect of understanding realistic variation in cognition. In addition, many bee species have successfully been reared in captive environments, allowing for individual experience to be controlled. Leveraging bee diversity alongside interdisciplinary approaches, combining ecology and cognition with neurobiology and genetics, will help us best understand abilities already revealed and reveal abilities yet to be discovered.

BOX 1: Ecology in bumblebee cognition

We highlight features of bumblebees' natural history that have already proved fruitful and that are worthwhile avenues for future exploration.

- Bumblebees attend to myriad cues, including scent, color, polarized light, texture, electrostatic field, humidity, and temperature. Previous work has set the stage for the exploration of prioritization and sensory integration of multimodal cues.
- Work on string-pulling indicates that bumblebees can learn novel behavioral routines without an understanding of the physical rules of the task [12]. Future work could test this phenomenon across the impressive range of natural flower morphologies.
- Experiments typically use sucrose solutions as a proxy for nectar, but flowers offer multiple, chemically and nutritionally complex rewards. Additional work on the impacts of complex rewards on bee cognition is needed [13].
- Cognition is most often tested in small-scale environments, but foragers and queens must navigate across vast environments searching for food and nest sites.
- Research has started to address the relationship between cognitive performance and fitness [9]. The utility of being able to test cognitive abilities in individual bees, while also allowing them to forage in wild or semi-wild scenarios, will lead to more discoveries in this realm.

Figure legend

Figure 1: The flexibility of bumblebee flower-visiting behavior. As generalist foragers, bumblebees will manipulate a variety of artificial and natural flowers to gain floral rewards such as nectar and pollen. A) Bumblebees attend to fine-scale pattern information from flowers, which may be the basis of their numerical skills; photo shows a bumblebee visiting a foxglove (photo: The Manic Macrographer). B) Bees visit flowers with complex floral displays, as illustrated by this passionflower (photo: Harald Steeg). C) Bumblebees must employ sometimes complex

motor routines to access floral rewards, as illustrated by a bee manipulating the banner and keel of a lupine flower (photo: Dave Angelini).

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