A queen bumble bee (Bombus impatiens) in a laboratory colony at the University of Texas at Austin

ALEX WILD

"Personality" Differences between Bees

Individuals of many insect species seem indistinguishable, interchangeable, mass-produced. Could each have a personality?

By Lars Chittka

The first behavioral scientist to systematically study individual differences in the psychology of invertebrates was zoologist Charles Henry Turner (1867–1923), who, as early as 1891 in his first paper on spider web construction, observed pronounced differences in how individual web spinners coped with unusual geometric challenges, and referred to one individual spider as the "master mind of the locality." The identification of such individual differences, which he discovered in invertebrates as diverse as spiders, ants, and cockroaches, is a constant theme in Turner's work.

We have learned in recent years that, in bees, differences occur in any psychological trait examined, and occur between individual bees (each of which will often respond similarly when tested repeatedly), as well as between colonies of bees in social species—unsurprisingly, since colonies are families of genetically related individuals. Different individuals have subtly different sensory equipment, which means they selectively perceive different aspects of their environment, and differences in brain structure, which determine that information is stored and used differently. Variation in individual intelligence is important for how well bees fare in the economy of nature, and variation among individuals of a colony determines the efficiency of their division of labor.

In the last twenty years, quantifying individual variation has been facilitated by new technologies, such as radio frequency identification (RFID)—the same technology that is used in pet microchipping or season tickets in many public transport systems. The moment bees are marked in ways that make them recognizable as individuals (for example, with number tags), a wholly new perspective on their nature opens up. It becomes instantly obvious that different individuals of the same species behave very differently. Some bees are more aggressive than others, some are harder working, some more intelligent; some make fast and sloppy decisions while others are more careful, and so on.

Variation among individuals and between colonies can be heritable—for example, a colony of especially fast learners might pass the trait on to the next generation. However, not all variation among individuals is heritable. The dramatic differences between honey bee queens and their sterile workers, for example, involve every aspect of their sensory system, brain structure, and behavior—but these are not caused by any differences in their DNA, since these castes are genetically identical. Instead, the differences between queens and workers are epigenetic and are prompted solely by environmental factors, such as the food they are given as larvae. Queen larvae get fed a special "designer diet"—the so-called royal jelly—in large quantities and over extended periods. This richly nutritious substance's chemical composition is only partially understood. It is produced by glands in the mouths of young nurse bees. All larvae are initially fed royal jelly, but worker larvae are soon weaned and switched to a diet of pollen and nectar, whereas queen larvae are bathed in royal jelly throughout their larval development and feed on it into adulthood. This differential rearing procedure results in striking morphological, behavioral, and physiological differences between these different castes.

Honey bee queens live for years, produce up to 2,000 eggs per day, and never visit flowers (or engage in any other activity of colony construction or maintenance), and their behavioral goals are entirely different from those of worker bees. These goals come with a wholly different psychology: much of the worker bee's mind is occupied with flower visitation, whereas a queen's desiderata are more Shakespearean: upon emergence from their pupae, new honey bee queens engage in a series of deadly duels with rival queens. The single survivor will leave the home for one to five mating flights, during which she visits drone congregating areas used solely for mating, which might be several kilometers from the hive, where hundreds of drones typically wait. Queens will mate with an average of twelve drones in flight; the drones die shortly afterward, since the explosive ejaculation ruptures the everted genitals. A mated queen then returns to her native hive; egg laying begins soon after, and she will typically not leave the colony again unless a new queen is raised in the subsequent year, in which case the old queen leaves the nest with a large swarm of workers to relocate to a new home.


A rarely witnessed killing of an old queen honey bee (Apis mellifera) by a new queen

GEES BEES HONEY COMPANY

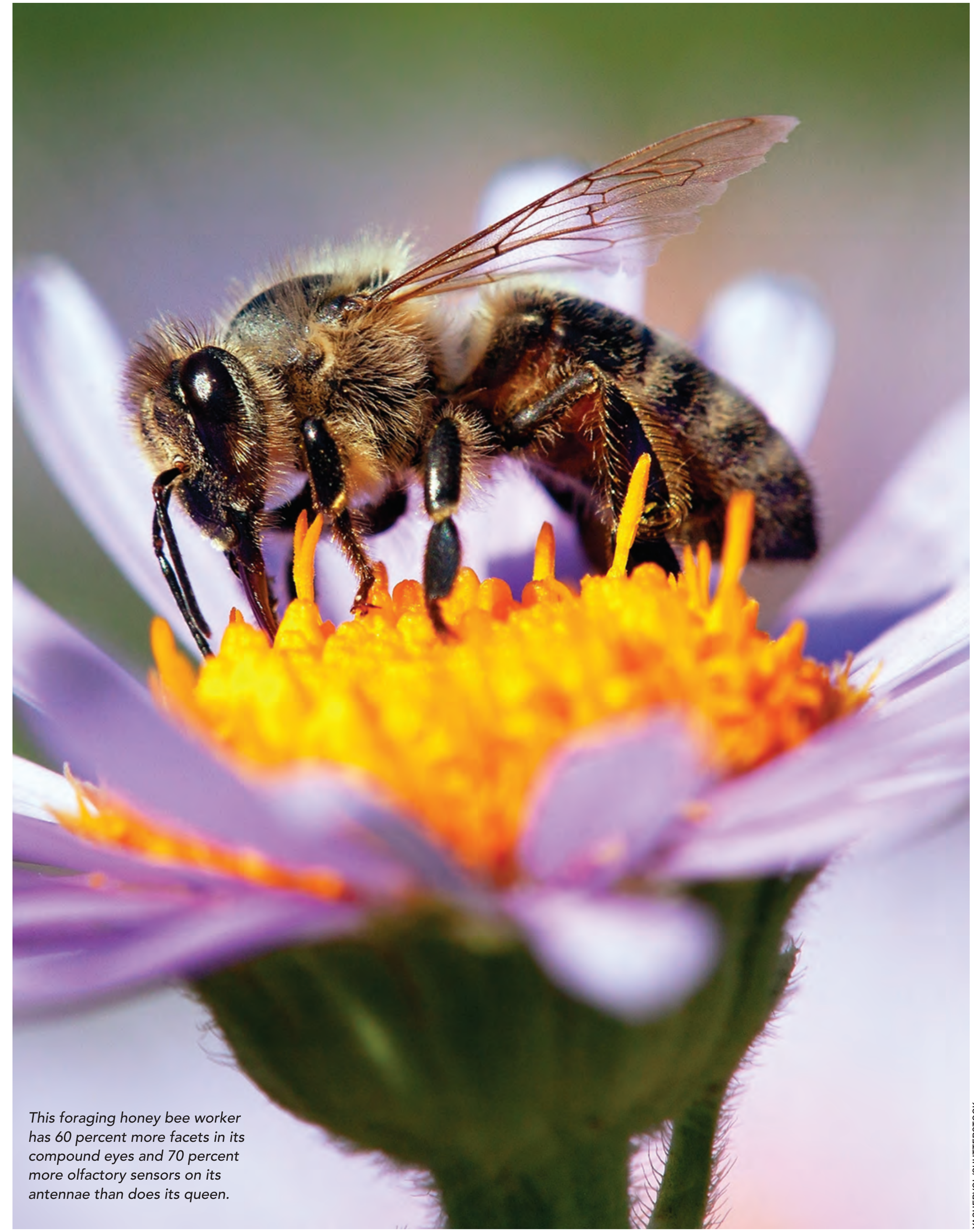
In stark contrast to a queen's life, the sterile honey bee workers typically live only for weeks, during which they engage in a series of specializations, among them the cleaning of comb cells (the first few days after emerging from the pupa), tending brood or the queen (~days 3–20), constructing wax combs (~days 7–20), guarding the nest entrance (~3 weeks of age), and foraging (typically 2–3 weeks of age) for various commodities such as nectar, pollen, water, and resin. On the other hand, workers will never know sex.

There are also striking differences in the sensory apparatus. Honey bee workers have 60 percent more facets in their compound eyes and 70 percent more olfactory sensors on their antennae than do queens. The many differences in the life span, specializations, behavior, sensory physiology, and brain anatomy of social insect queens and workers—often solely as a result of the difference in larval rearing—are perhaps one of nature's most extreme examples of the influence of the environment on an individual's fate.

The changes from one task specialization to another within an individual's life span are also reflected in brain anatomy. For example, the transition from within-hive duties to foraging in workers is accompanied by drastic (15–20 percent) enlargements in the mushroom-shaped bodies of their brains, presumably as a result of having to memorize large amounts of information about the spatial foraging environment and the features of rewarding flowers. However, some of this growth happens shortly before the age at which bees are destined to leave the hive to forage. This indicates that the bees' inborn developmental programs prepare the brain for outdoor flight by increasing memory storage capacity.

The success of insect societies has often been attributed to their labor division and specialization. However, with the exception of rigid castes, such as egg-laying queens or termite "soldiers," specialists are often not distinct in morphology, and indeed are largely totipotent in terms of the tasks they can potentially perform. Even though social insect specialists might perform the same routine for extended periods, they can typically switch to other activities should these become necessary. Early in the nineteenth century, naturalist François Huber (1750-1831) proposed a groundbreaking idea of how this might come about by simple self-organization, without the need for a powerful decision maker allocating workers to one task or another.

Huber was interested in climate control in honey bee hives, and specifically the question of how they kept the hive well ventilated to avoid suffocation. He found that with decreasing oxygen levels more bees would stand still and whir their wings for ventilation—when the air was extremely stuffy, all workers would do so. Huber hypothesized that individual honey bees were differentially sensitive to noxious smells, and that those most sensitive would be the ones to initiate fanning first. Should conditions nonetheless deteriorate, more individuals' tolerance thresholds would be reached, and they would begin fanning too. In this way, a decentralized allocation of the appropriate numbers of workers to the job of ventilation would be assured in all areas of the hive. Huber could not test this elegant hypothesis, since his team had no means of marking individual


This foraging honey bee worker has 60 percent more facets in its compound eyes and 70 percent more olfactory sensors on its antennae than does its queen.

YASHERVOL/SHUTTERSTOCK

Close-up of the head of a bumble bee (Bombus terrestris) with its large eyes and antennae

YASHERVOL/SHUTTERSTOCK

of one species that you might see in a colony or on flowers are not related to age. Instead, such variation is the result of differences in the amount of nutrition received during larval development. Bees do all their growing while they are helpless, legless grubs sitting in brood cells.

In adults, there is no strict division of labor in accordance with body size in the bumble bee colony, but there is a tendency for the smallest workers to engage more within-nest duties, such as wax construction and brood rearing, whereas large workers tend to be those that leave the nest to visit flowers. In a 2002 paper in the international journal, *Insectes Sociaux*, entomologists Johannes Spaethe, now at the University of Würzburg, and Anja Weidenmüller, now at the University of Konstanz, report on their discovery that the largest workers in the buff-tailed bumble bee species (*Bombus terrestris*) are also the most efficient workers. This is not, however, just the result of physical strength, which might make them better flyers and more efficient at manipulating flowers. It turns out that larger workers also have a superior sensory apparatus.

bees. Today, there is ample experimental evidence that the flexible way in which bee colonies allocate workers to the relative urgency of the many vital tasks is, indeed, mediated, at least in part, by different individual sensitivities to the stimuli that indicate the respective needs.

Individual sensory thresholds were first experimentally determined by ethologist and Nobel Laureate Karl von Frisch (1886-1982), as reported in his 1934 paper in the *Journal of Comparative Physiology*, "Über den Geschmachsinn der Bienen" ("The Honey Bee's Sense of Taste"), which contains a two-page section headlined "Individualität" (individuality). Von Frisch tested bees' readiness to accept low-concentration sugar solutions, or solutions that had been laced with adverse tastants, such as hydrochloric acid. He observed individual bees for up to twenty-four days, and discovered that some bees were uniquely and consistently picky about the minimum sweetness levels they would tolerate, or singularly sensitive to acids or bitter substances. In fact, one individual appeared superlatively sensitive to all tastants that von Frisch tried. It was later discovered by Arizona State University entomologist Robert Page that differences in sensitivity to sugar are already manifest when bees are just a few hours old, and determine, for example, whether individuals become pollen or nectar foragers weeks later.

Unlike honey bees, whose workers are all roughly the same size, bumble bee workers inside a single colony can vary drastically in size—by more than a factor of ten—from the smallest, house fly-size workers to some that are practically the size of a queen. Bees don't grow once they have emerged from the pupa, so differences in size of bumble bees

Spaethe discovered that larger workers do not just have larger eyes. Their compound eyes also have larger facets (larger lenses) that convey higher light sensitivity, and this allows them to forage in dimmer ambient light conditions—for example, early in the morning before sunrise, when most other pollinators are asleep. In addition, by means of a sophisticated technique for shining light beams through the optical apparatus of bumble bee eyes, Spaethe discovered that larger bumble bees also have the advantage of seeing higher- resolution images, which allows them to detect smaller flowers, and from a greater distance. In fact, because larger bees carry bigger, higher-resolution eyes, a 33 percent increase in body size is accompanied by doubled precision in flower detection.

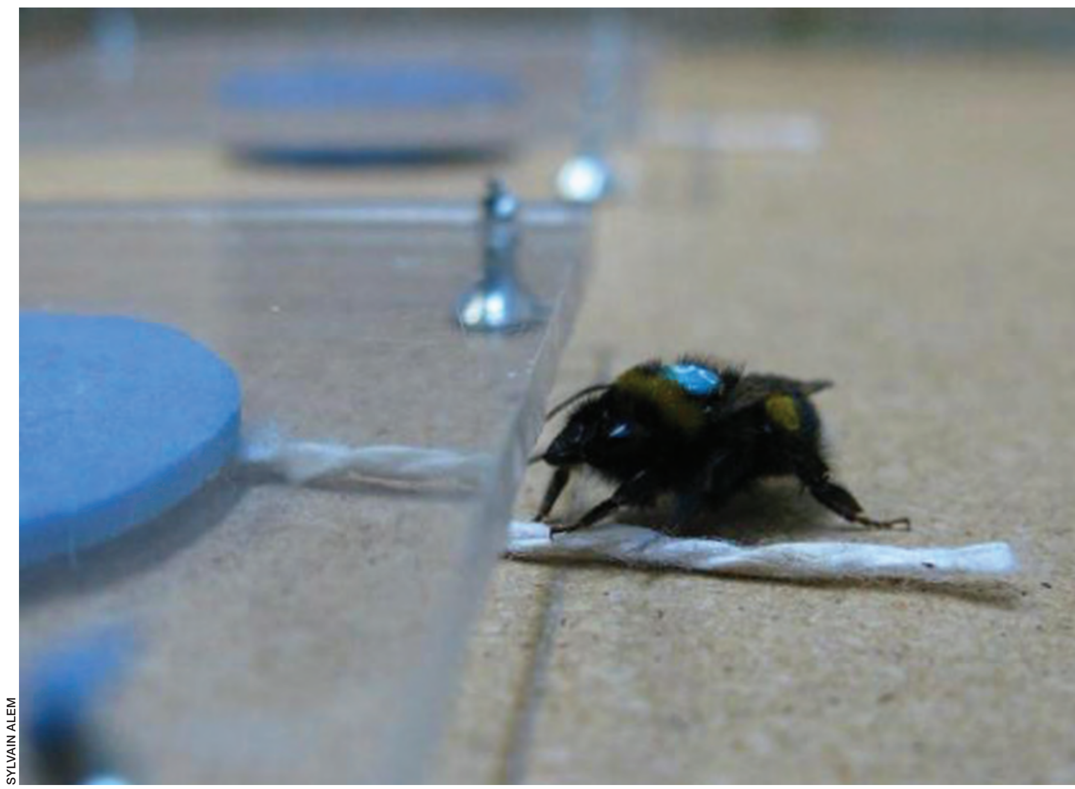
Spaethe also discovered that larger bumble bee workers have a keener sense of olfaction: their antennae have a higher number, and indeed a higher density, of olfactory sensors, which means that they can also detect floral scents from substantially greater distances. In other words, the (at least partially random) processes that lead to some larvae having better access to food result in pronounced differences in how the adults perceive the world, and determine their later work specialization.

In social bees, just as in human societies, the choice of "profession," or efficiency at a particular task, is only partially a result of innate predisposition, as determined by sensory thresholds, "talent," or innate tendency to engage in a job. It is also a result of perfecting skills through experience. Contrary to humans, however, there is likely no feedback from other bees about task performance. We don't yet have direct evidence that personally experienced success at a certain task determines the job an individual takes on in the colony longer-term.

My team also explored individual signatures under field conditions. We followed the entire foraging careers of individual bumble bees with radar, from their maiden flight through their discovery and exploitation of flower resources to their death. We encountered an individual that, after two early exploration flights, only visited two foraging locations over her entire life. Another bumble bee never settled on a single foraging patch during her life; almost every one of her foraging bouts was exploratory in nature, even though plenty of rich flower patches were available, and other bees returned to them regularly. It is doubtful that this individual ever contributed much to the communal pantry of the nest, but it is also conceivable that such intrepid explorers sometimes stumble onto a resource so rich that its exploitation might make a major difference to the home colony.

One psychological trait in which individual variation was observed in insects, before any other nonhuman animals, concerns the so-called speed-accuracy tradeoff. Turner observed in 1913 that among cockroaches trained to navigate mazes, younger individuals tended to be fast and error-prone, whereas older ones were slower but made fewer errors. Generally speaking, in any difficult discrimination task (such as telling apart two similar colors, patterns, or numbers), one can place emphasis on accuracy, but this may take an extended inspection time, or on speed—in which case accuracy may suffer. In bumble bees, we found no age differences in this regard, but we did find that there are differences between individual bees in how they go about this problem: some bees are consistently fast and sloppy, whereas others are more careful, slow, and accurate in their decision-making. Since individuals with different preferences for speed or accuracy might fare better or worse under different ecological conditions, the colony as a whole might fare best by harboring a diversity of individuals with different strategies.

When one performs experiments on the learning behavior of bees, there are often one or two "genius individuals" that solve a problem more quickly than all others, or in an exceptionally efficient way, or in ways wholly unexpected by the experimenters. In one experiment in which we measured the foraging efficiency of bumble bees in the wild, we weighed each bee upon departure from the nest, and again on its return, so that from the weight difference we could judge how much nectar it had collected. This required us to capture each bee briefly upon its departure from the nest in a black plastic container, and again on the return from the foraging bout. Most bees showed some reluctance to be caught; some displayed mild aggression, though eventually



SYLVAIN ALEM

A blue artificial flower, with a sucrose solution in a center well, is placed under a clear Plexiglas table, so a bumble bee can see the flower, but cannot reach the well, because the gap between the Plexiglas table and the floor is too small. To gain access to the well and its reward, the bumble bee must pull a string. Here, a bumble bee has placed its left front foot on the string to pull it.

they got used to the procedure. One individual, however, would regularly fly directly into the black container, even if an experimenter held the container overhead meters away from the hive: this bee had essentially come to view the container as a "public transport" vehicle and expected to be carried back to the nest inside it.

The individuals that are exceptionally innovative at problem solving are typically those whose behavior is the most variable, and which thus appear more exploratory than others. In this way, intelligence is linked to behavioral variability. Neuroscientist Björn Brembs, of the University of Regensburg in Germany, makes a convincing case that fully hardwired, predictable behavior is a sure path to extinction. For example, if an animal behaves in a fully foreseeable manner when confronted with a predator, the predator will eventually figure this out. Having some—though not unlimited—noise in the nervous system means that behavior always has some level of variability. Those individuals with more strongly pronounced behavioral variability will experiment with more solutions to a problem, and will thus ultimately be more efficient problem solvers.

This became apparent in our experiments with string-pulling bumble bees, in which bees had to pull a thread to get access to an artificial flower placed under a plexiglass table. The vast majority of individual bees (over 100 in this case) either required stepwise training, or had to observe other bees solving the task before they managed it themselves. Two individuals, however, solved the task spontaneously, and it was clear from our video recordings that these were especially exploratory individuals, who tried tirelessly to reach under the plexiglass table from a variety of positions, using various body postures, until their feet caught hold of the string, causing a visible flower movement that prompted them to elaborate on the technique.

In other experiments, which do not require a specific innovation or insight from the subjects, the differences among individuals are more of a gradation—quantitative rather than qualitative. In such tests, it is possible to assign numerical values to individuals' performances, for example by quantifying and comparing learning speed in the same task (such as learning that one artificial flower type is rewarding and another is not). By following each individual bee's learning progress over time, and measuring how it improves with experience, one can use mathematical tools to fit curves to each bee's learning behavior.

Color-learning ability can be linked to natural foraging success and also correlates with other measures of learning. Such learning occurs in the bee's mushroom bodies—an insect brain area that contains the principal association centers. Many axons from the visual centers (optic lobes) of the brain terminate in the mushroom bodies. In the same input region, there are endings of the neural reward pathway, which signals when a sweet reward is perceived by the bee's mouthparts. The connections between these two sensory inputs are synaptic complexes called "microglomeruli"—which can be modified in number and strength from learning if visual information coincides with reward.

We found that bees with high densities of microglomeruli were not only faster learners, but also had more durable memories. Likewise, the density of microglomeruli in this region increased as a result of experience, especially when the bees had to learn that several colors were linked to reward, whereas several other colors were not. Thus, the fastest learners may be those that have more microglomeruli to start with and build further microglomerular connections as experience accumulates.

Just as there are "personality" differences among individual bees, there can be even greater differences between colonies of social bees. Each colony has its own behavioral signature. Some hives are uniquely aggressive, while others may be particularly good honey producers. There are also various aspects of cognition, such as learning speed, that differ between colonies.

We tested a large number of individual worker bees of twelve bumble bee colonies in a flower-color-learning task where one color was linked to sugary rewards and the other was not. Learning curves were measured for each bee under controlled laboratory conditions, and once we had tested enough bees from each colony, we then placed the same colonies in the open, so they faced the real-life challenges of locating and learning about suitable flowers in the colonies' large flight ranges. The results were striking. Colonies varied in learning speed by a factor of nearly five, and the colonies dominated by the slowest learners collected 40 percent less nectar than the colonies containing, on average, faster learners. This indicates that high learning speed might confer substantial advantages under natural conditions. On the other hand, even members of the slowest-learning colony didn't come home entirely empty-handed, suggesting that the most rapid learners don't deplete all the goods.

If natural selection favors faster learners, why are there any slow learners left in the wild at all? Are there some disadvantages to making associations rapidly that might allow slow learners to persist under natural conditions for many generations?

We explored this question from many angles. For example, we wondered whether rapid learning might lead to such tight associations that it might interfere with the acquisition of new information when previously learned contingencies are reversed, such as when a previously rewarding flower species or patch has been overexploited and is tapped out, and another, previously poorly rewarding species ups its nectar secretion and is now a food bonanza.

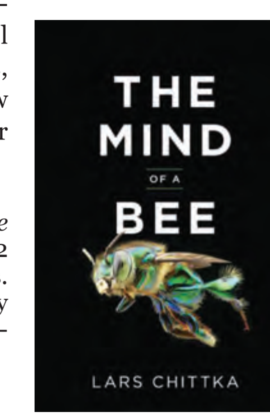
Worker bees tending a brood

CLARE FLYNN

But it turned out that those individuals that learned rapidly were also swift at reversing their associations. We also found that bumble bees that were good at learning colors also tended to excel at learning shapes and odors: again, there seemed to be no tradeoff between performance at one task and at another; instead, smart individuals tended to perform well at all tasks.

Taken together, these findings made the persistence of slow learners in the wild an even bigger mystery. If fast learning is strongly advantageous in the wild, and has no costs, why do we still see slow learners at all? One potential clue came from a study by biologist Nigel Raine and his team at the University of Guelph, in Ontario, Canada, in which it was found that faster-learning bumble bee individuals were active for fewer days of their short lifespan than were slow learners, and this effect was so pronounced that over a lifetime, the "dumber" individuals actually contributed more to colony foraging success. Perhaps the reduced foraging activity in the smarter bees was a result of an energetic cost of rapid learning.

To conclude, we have seen that there are immense differences in sensory systems, behavior, and learning among individual bees and between colonies. Viewing bees as beings with unique "personalities," possessing individual preferences, learning abilities, and memories also lends a new perspective to the need for their conservation.



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