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IN THE EARLY 1990S, WHEN I WAS A PH.D. STUDENT AT THE FREE UNIVERSITY of Berlin modeling the evolution of bee color perception, I asked a botany professor for some advice about flower pigments. I wanted to know the degrees of freedom that flowers have in producing colors to signal to bees. He replied, rather furiously, that he was not going to engage in a discussion with me, because I worked in a neurobiological laboratory where invasive procedures on live honeybees were performed. The professor was convinced that insects had the capacity to feel pain. I remember walking out of the botanist's office shaking my head, thinking the man had lost his mind.

Back then, my views were in line with the mainstream. Pain is a conscious experience, and many scholars then thought that consciousness is unique to humans. But these days, after decades of researching the perception and intelligence of bees, I am wondering if the Berlin botany professor might have been right.

Researchers have since shown that bees and some other insects are capable of intelligent behavior that no one thought possible when I was a student. Bees, for example, can count, grasp concepts of sameness and difference, learn complex tasks by observing others, and know their own individual body dimensions, a capacity associated with consciousness in humans. They also appear to experience both pleasure and pain. In other words, it now looks like at least some species of insects—and maybe all of them—are sentient.

These discoveries raise fascinating questions about the origins of complex cognition. They also have far-reaching ethical implications for how we should treat insects in the laboratory and in the wild.

SIGNS OF INTELLIGENCE

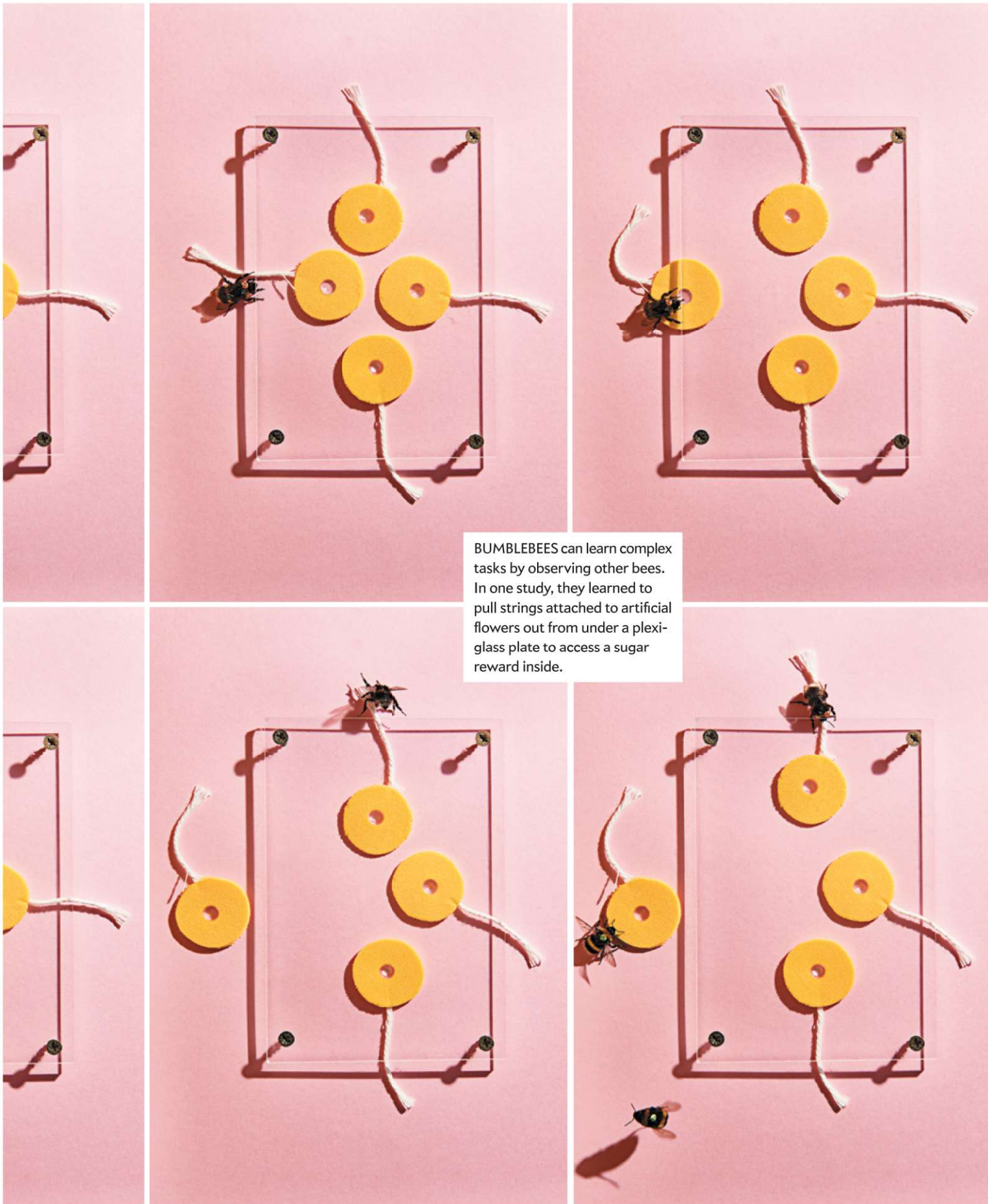
THE CONVENTIONAL WISDOM about insects has been that they are automatons—unthinking, unfeeling creatures whose behavior is entirely hardwired. But in the 1990s researchers began making startling discoveries about insect minds. It's not just the bees. Some species of wasps recognize their nest mates' faces and acquire

impressive social skills. For example, they can infer the fighting strengths of other wasps relative to their own just by watching other wasps fight among themselves. Ants rescue nest mates buried under rubble, digging away only over trapped (and thus invisible) body parts, inferring the body dimension from those parts that are visible above the surface. Flies immersed in virtual reality display attention and awareness of the passing of time. Locusts can visually estimate rung distances when walking on a ladder and then plan their step width accordingly (even when the target is hidden from sight after the movement is initiated).

Given the substantial work on the sophistication of insect cognition, it might seem surprising that it took scientists so long to ask whether, if some insects are that smart, perhaps they could also be sentient, capable of feeling. Indeed, the question had been on my mind for decades. Since the early 2000s I have used it in debates for undergraduate student group tutorials. I viewed it as a thought-provoking intellectual exercise, but the discussions invariably ended with the conclusion that the question is formally unanswerable. We have no direct window into the inner world of an animal that cannot verbally communicate its thoughts and feelings—which is to say, all nonhuman animals. The question of whether insects are sentient remained academic.

I began to think the issue had real-life relevance when, 15 years ago, Thomas Ings, now at





BUMBLEBEES can learn complex tasks by observing other bees. In one study, they learned to pull strings attached to artificial flowers out from under a plexi-glass plate to access a sugar reward inside.

Anglia Ruskin University in England, and I performed an experiment in which we asked whether bumblebees could learn about predation threat. Certain spider species called crab spiders perch on flowers to catch pollinating insects, including bees. We built a plastic spider model with a mechanism that would briefly trap a bumblebee between two sponges before releasing it. The bumblebees showed a significant change in their behavior after being attacked by the robotic spider. Perhaps unsurprisingly, they learned to avoid spider-infested flowers and meticulously scanned every flower before landing. Curiously, however, they sometimes even fled from imaginary threats, scanning and then abandoning a perfectly safe, spider-free flower. This false-alarm behavior resembled symptoms of post-traumatic stress disorder in humans. Although this incidental observation did not constitute formal evidence of an emotionlike state, it did move the possibility of such states in insects into the realm of possibility.

Other research hinted that insects might also have positive states of mind. Many plants contain bitter substances such as nicotine and caffeine to deter herbivores, but these substances are also found in low concentrations in some floral nectars. Researchers wondered whether pollinators might be deterred by such nectars, but they discovered the opposite. Bees actively seek out drugs such as nicotine and caffeine when given the choice and even self-medicate with nicotine when sick. Male fruit flies stressed by being deprived of mating opportunities prefer food containing alcohol (naturally present in fermenting fruit), and bees even show withdrawal symptoms when weaned off an alcohol-rich diet.

Why would insects consume mind-altering substances if there isn't a mind to alter? But these suggestive hints of negative and positive mind states still fell short of what was needed to demonstrate that insects are sentient.

PLEASURE AND PAIN

I BEGAN TO CONSIDER how one might more directly test emotionlike states in insects. So-called cognitive bias tests have been developed to evaluate the psychological welfare of animals such as rats that live in captivity. These tests are essentially versions of the proverbial glass that can be half-full or half-empty: optimistic humans might view the ambiguous glass as nearly full, whereas pessimists would judge the same glass as being nearly empty. My collaborators and I decided to develop a similar test for bees.

We trained one group of bees to associate the color blue with a sugary reward and green with no reward, and another group of bees to make the opposite association. We then presented the bees with a turquoise color, a shade intermediate between blue and green. A lucky subset of bees received a surprise sugar treat right before seeing the turquoise color; the other bees did not. The bees' response to the ambiguous stimulus depended on whether they received a treat before the test: those that got the pretest sugar approached the intermediate color faster than those that didn't.

The results indicate that when the bees were surprised with a reward, they experienced an optimistic state of

mind. This state, which was found to be related to the neurotransmitter dopamine, made the bees more upbeat, if you will, about ambiguous stimuli—they approached it as they would the blue or green colors they were trained to associate with a reward. It also made them more resilient toward aversive stimuli, as occurs in humans: bees that were given a surprise dose of sugar recovered faster when ambushed by a fake predator, taking less time to reinitiate foraging than their peers that did not receive sugar before the simulated attack.

Other work suggests that bees can experience not only optimism but also joy. Some years ago we trained bumblebees to roll tiny balls to a goal area to obtain a nectar reward—a form of object manipulation equivalent to human usage of a coin in a vending machine. In the course of these experiments, we noticed that some bees rolled the balls around even when no sugar reward was being offered. We suspected that this might be a form of play behavior.

Recently we confirmed this hunch experimentally. We connected a bumblebee colony to an arena equipped with mobile balls on one side, immobile balls on the other, and an unobstructed path through the middle that led to a feeding station containing freely available sugar solution and pollen. Bees went out of their way to return again and again to a “play area” where they rolled the mobile balls in all directions and often for extended periods without a sugar reward, even though plenty of food was provided nearby. There seemed to be something inherently enjoyable in the activity itself. In line with what other researchers have observed in vertebrate creatures at play, young bees engaged more often with the balls than older ones. And males played more than females (male bumblebees don't work for the colony and therefore have a lot more time on their hands). These experiments are not merely cute—they provide further evidence of positive emotionlike states in bees.

All this research raised the more uncomfortable question of whether bees might also be capable of experiencing pain. Investigating this issue experimentally presents researchers with a moral dilemma: if results are positive, the research might lead to improved welfare of trillions of wild and managed insects. But it would also involve potential suffering for those animals that are tested to obtain the evidence. We decided to do an experiment with only moderately unpleasant stimuli, not injurious ones—and one in which bees could freely choose whether to experience these stimuli.

We gave bees a choice between two types of artificial flowers. Some were heated to 55 degrees Celsius (lower than your cup of coffee but still hot), and others were not. We varied the rewards given for visiting the flowers. Bees clearly avoided the heat when rewards for both flower types were equal. On its own, such a reaction could be interpreted as resulting from a simple reflex, without an “ouch-like” experience. But a hallmark of pain in humans is that it is not just an automatic, reflexlike response. Instead one may opt to grit one's teeth and bear the discomfort—for example, if a reward is at stake. It turns out that bees have just this kind of flexibility. When the

rewards at the heated flowers were high, the bees chose to land on them. Apparently it was worth their while to endure the discomfort. They did not have to rely on concurrent stimuli to make this trade-off. Even when heat and reward were removed from the flowers, bees judged the advantages and disadvantages of each flower type from memory and were thus able to make comparisons of the options in their minds.

This finding alone is not a decisive proof that bees experience pain, but it is consistent with that notion, and it is only one of several indicators. Bees and other insects also form long-term memories about the conditions under which they were hurt. And they have specialized sensors that detect tissue damage and are connected to brain regions that also process and store other sensory stimuli. These creatures have the necessary neural equipment to modulate pain experiences by top-down control. That is, they are not constrained by simple reflex loops when responding to noxious stimuli but display the flexibility to modify their responses according to current circumstances, in the same way as we can choose to press a hot door handle to escape a burning building.

Critics could argue that each of the behaviors described earlier could also be programmed into a nonconscious robot. But nature cannot afford to generate beings that just pretend to be sentient. Although there is still no universally accepted, single experimental proof for pain experiences in any animal, common sense dictates that as we accumulate ever more pieces of evidence that insects can feel, the probability that they are indeed sentient increases. For example, if a dog with an injured paw whimpers, licks the wound, limps, lowers pressure on the paw while walking, learns to avoid the place where the injury happened and seeks out analgesics when offered, we have reasonable grounds to assume that the dog is indeed experiencing something unpleasant.

Using a similar logic, my colleagues and I reviewed hundreds of studies from the literature across several orders of insects to search for evidence of a capacity to feel pain. [Our analysis](#) revealed at least reasonably strong evidence for this capacity in a number of taxa, including cockroaches and fruit flies. Crucially we also found no evidence that any species convincingly failed any criterion for pain-like experiences. It appears that in many cases, scientists simply haven't looked thoroughly enough for indications that the insect species they study experience discomfort.

AN ETHICAL OBLIGATION

IF AT LEAST SOME INSECTS are sentient and can feel pain, as appears to be the case, what are the implications of that revelation? I sometimes get asked questions along the lines of "Does this mean that I can't kill a mosquito that lands on my arm, even though it might infect me with a life-threatening disease?" No, it does not mean that. The insight that many conventional livestock animals are probably sentient hasn't stopped humans from killing them. But it has resulted in an awareness (and legislation in many countries) that this should be done in such a way as to minimize distress and pain. If death is



A QUEEN BUMBLEBEE and workers tend a nest. Open wax structures are honey or pollen pots; closed structures contain larvae.

instantaneous, such as when you slap the mosquito on your skin, there is little room for suffering. Setting ants alight with a magnifying glass, as children are sometimes taught to do for fun, is a different matter.

The treatment of insects in scientific laboratories also deserves consideration. Insects transmit some of the deadliest human diseases, so research into how they can be controlled is obviously important. In addition, we could develop remedies for a variety of human health disorders by studying their molecular genetic and neurobiological underpinnings in insects such as fruit flies. Researchers are often encouraged by funding agencies to work on insects rather than vertebrates in part because there are supposedly no ethics to consider. But some of the methods used to study them have the potential to cause intense distress. Insects are sometimes embedded in hot wax after their extremities are removed, their head capsules are then opened and electrodes inserted into various parts of their brain—all done without anesthesia.

Scientists with whom I have discussed the topic have sometimes countered that we still haven't delivered irrefutable proof that insects can suffer. This is factually accurate, but given what we now know about the plausibility of pain experiences in some insects, wouldn't we instead want to be reasonably certain that specific invasive treatments do *not* cause suffering? We urgently need more research into this question and into the identification and development of suitable anesthetics.

Some of my colleagues are worried about the introduction of vertebrate-style legislation and paperwork for

work on insects. I understand their concern. Politics has a way of turning well-intentioned recommendations from scientists into bureaucratic nightmares, which can hobble scientific progress while bringing about no appreciable benefits for animal welfare. A potentially more valuable approach would be if insect researchers themselves took the lead in considering how to minimize suffering, to reduce numbers of insects tested or sacrificed when possible, and to ensure that the severity of procedures is proportional to knowledge gain in both curiosity-motivated and applied research.

Insects are used on a far grander scale in the feed-and-food industry. More than a trillion crickets, black soldier flies, mealworms and other species are killed annually, and the sector is expanding rapidly. Often touted as a replacement for some or all the vertebrate meat in people's diets, insect farming is considered an environmentally friendly alternative to the conventional farming of livestock such as cattle or chickens. Another perceived advantage of insect farming is that there are supposedly no ethical concerns with insects like there are with cows and chicken. In fact, some insect-farming companies specifically promote the notion that insects lack any capacity for pain.

This claim is demonstrably incorrect for all insect species tested so far. Science tells us that the methods used to kill farmed insects—including baking, boiling and microwaving—have the potential to cause intense suffering. And it's not like they're being sacrificed for a great cause. The bulk of the industry does not actually seek to replace human consumption of vertebrate meat with insects. Instead most of the slaughtered insects go to feeding other animals that are farmed for human consumption, such as salmon or chicken. In other words, farmed insects are being used to turbocharge, not replace, the conventional livestock production.

But even if replacing vertebrate meat was the goal, we need scientific evidence for what constitutes humane slaughtering methods and ethically defensible rearing conditions for insects. It is possible that such evidence will reveal less capacity for suffering in some larval stages of some species, but until we have that evidence, we should err on the side of caution.

Unfortunately, a vegetarian or vegan diet is not necessarily free of ethical concerns for the welfare of insects either. Many insects share our taste for the leaves, roots, vegetables and fruits of the plants that we consume. As a result, several million metric tons of pesticides are deployed every year worldwide to streamline the production of cheap food for maximum profit. These pesticides poison and kill countless insects (and many other animals), often by slow processes lasting several days.

The plant-eating insects are not the only ones affected. The adverse effects of the insecticides known as neonicotinoids on bees are well documented. Although their concentration in flower nectar and pollen is typically too low to kill instantly, these insecticides affect learning, navigation, foraging efficiency and reproductive success, severely impacting populations of wild bees. This collateral damage to bees is viewed as concerning because

these are beneficial insects with an important utility for us humans: they pollinate our crops and garden flowers. But these pesticides also have the potential to cause mass suffering in bees and other insects—another reason to ban, or at least strongly limit, their use.

Bees in particular face additional stress from commercial pollination operations. Mass production of raspberries, blueberries, apples, tomatoes, melons, avocados and many other kinds of produce is dependent on honeybees or bumblebees being commercially mass-reared, bred, farmed and shipped to distant locations to pollinate the crops.

Almond milk, a popular alternative to dairy milk, relies to a large extent on the California almond bloom, one of the biggest commercial pollination events in the world. Migratory beekeepers load more than half of North America's honeybees (several dozen billion individuals) on trucks to be shipped to 800,000 acres of almond tree monoculture in California during the flowering period, then ship the bees back to their original locations or other crop-flowering events.

The "colony collapse disorder" that you may have heard about in the media is not just the result of some well-known pathogens but also of honeybees being literally stressed to death by ruthless beekeeping practices. Even brief shaking of bees induces a pessimistic emotionlike state. Now imagine the effects of intense and prolonged vibrations imposed on bees when they are trucked across continents in sealed hives, sustained on artificial food and unable to defecate outside the hive, then typically finding themselves in crop monocultures that lack the diversity of floral food bees normally require. Scientists have extensively studied the detrimental effects of stress on the immune system in several species, including insects. For invertebrate creatures such as insects, researchers have generally assumed the stress is strictly physiological, like a plant wilting when deprived of water. The possibility that in insects stress is at least partly psychological in nature deserves further exploration.

To live, to eat, we almost inevitably kill other living things, even if our labor division means that you personally don't do the killing. But to the extent that the affected creatures are probably sentient, we have a moral obligation to minimize their suffering—whether in research labs, on feed-and-food farms, or in agricultural settings.

The fact that to date there is no smoking-gun type of proof for any animal's sentience does not mean we're off the hook. On the contrary, the reasonably strong psychological, pharmacological, neurobiological and hormonal indicators of sentience that we now have for many animals, including some insects, mean that acquiring evidence in the opposite direction is in order. We should demand reasonably strong evidence of the absence of sentience before subjecting them to interventions that have the potential to cause intense distress. ■

FROM OUR ARCHIVES

The Mind-Boggling Math of Migratory Beekeeping. Ferris Jabr; ScientificAmerican.com, September 1, 2013.

[scientificamerican.com/magazine/sa](https://www.scientificamerican.com/magazine/sa)



BEE JOY:
In another
experiment,
bees chose
to roll balls
around rather
than visiting
feeding stations—
a form of play.