In hives, graduating to forager a requirement for social membership

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Graduate student Cassondra Vernier conducted lab experiments and observed hours of bee interactions at the entrance to the hive. She is shown here at Tyson Research Center, Washington University's environmental field station. Credit: Washington University in St. Louis

It is a classic coming-of-age story, in many ways.

A honey bee hatches and grows up deep inside a hive. Surrounded by 40,000 of her closest relatives, this dark and constantly buzzing place is all that she knows. Only after she turns 21 days old does she leave the nest to look for pollen and nectar. For her, this is a moment of great risk, and great reward.

It's also the moment at which she becomes recognizable to other bees, according to new research from Washington University in St. Louis. A study in the journal *eLife* reports that honey bees (Apis mellifera) develop different scent profiles as they age, and the gatekeeper bees at the hive's door respond differently to returning foragers than they do when they encounter younger bees who have never ventured out before.

This work offers new insight into one of the most important interactions in the lives of social insects: recognizing self and other.

Until this point, most bee researchers thought bees recognize and respond to a scent that is the homogenized scent of all of the members of their own colony. That's how it works for some ants and other insects, at least. But new work from the laboratory of Yehuda Ben-Shahar, associate professor of biology in Arts & Sciences, shows that nestmate recognition instead depends on an innate developmental process that is associated with age-dependent division of labor. The work was completed in collaboration with researchers from the lab of Joel Levine at the University of Toronto.

"It was always assumed that the way that honey bees acquire nestmate recognition cues, their cuticular hydrocarbon (CHC) profiles, is through these mechanisms where they rub up against each other, or transfer

compounds between each other," said Cassondra L. Vernier, a graduate student at Washington University and first author of the new study.

"You would expect, then, that even younger bees would have a very similar pheromonal profile as older bees. When in fact that is not what we saw," she said.

Vernier compared the CHC profiles of bees on the day they were born and at 1 week, 2 weeks, and 3 weeks old. The 3-week-old bees had significantly different profiles than their younger siblings.

A 3-week-old foraging bee also has a very different job to support the hive than a younger bee—one who spends her time as a nurse caring for bee larvae and building the waxy honeycomb structures in the hive.

The researchers wanted to separate out whether the differences they saw were based on age alone, or were somehow tied to the older bees' foraging activities. Bees that exit the hive to collect nectar encounter lots of scents on flowers and other surfaces they touch. They also are exposed to different environmental factors such as sunshine and rain that could affect their body coatings.

So Vernier also compared the CHC profiles of foraging-age bees that were held in the hive and not permitted to forage with bees that were able to venture out. These two groups were also significantly different.

"What we found is that it's actually a combination of both—of being at the age for foraging, and actually performing the foraging activities," said Ben-Shahar.

Guards are gatekeepers; specific triggers still unknown

Importantly, not every bee notices the difference in scent profiles. Guard bees are the only ones who care to identify outsiders.

"They sit in the entrance and they have a very specific posture," Ben-Shahar said of the guards. "They're very attentive. Their forelegs are usually raised, and they're very alert. Still, it is hard to know who they are until they react to somebody."

Place a 1-day-old, 1-week-old, or 2-week-old outsider on the stoop in front of a guard, and she is likely to be able to waltz on through. But it's a different story after 3 weeks of age—when guards bite, sting and/or drag outsiders away from the door.

"Nestmate recognition is something that is very context-specific. It involves an interaction between very specific bees within the colony," Ben-Shahar said. "Most bees are completely oblivious. Most colony members don't produce the signal that tells anyone if they belong or not, and they don't care about the signal. They don't react to it."

As an important caveat, the new study does not directly address the mechanism by which cue specificity is determined in bees. Which specific components of the honey bee CHC profile represent the nestmate recognition cue remains unknown.

"Something environmentally related is causing expression-level changes in the CHC profiles of the bees," Vernier said. "That's our model for now."

More information: Cassondra L Vernier et al. The cuticular hydrocarbon profiles of honey bee workers develop via a socially-modulated innate process, *eLife* (2019). DOI: 10.7554/eLife.41855