Notes from the Lab: The Latest Bee Science Distilled

by Scott McArt

A glimpse into the architectural talents of honey bees

My kids love building with Legos. So much that I built them a giant Lego table that takes up about a quarter of our living room. On that table, I get to watch their architectural talents revealed, or perhaps *improved* is a better word, from one day to the next.

Each time I open up one of my honey bee colonies, I think the same thing. There's almost always new comb that's been built, allowing me to marvel at the bees' architectural talents. While most comb is made up of spectacularly efficient worker-sized hexagons (more on that later), there's always something that isn't regular hexagons. A transition from worker to drone cells, merging of worker cells with slightly different orientations, or something else.

But are honey bees actually architects, or do individual bees simply stumble along, building one cell and then another, eventually ending up with a comb? How common are irregularly shaped cells? Are irregular cells made individually or in predictable combinations? Is there a common tactic for how transitions are made across a comb? In other words, do honey bees have a repertoire of building behaviors that suggest cognitive, architect-like processes are at play? These are the topics for our forty-sixth Notes from the Lab, where we summarize ***"Imperfect comb construction reveals the architectural abilities of honeybees,"*** written by Michael Smith and colleagues and published in the journal ***Proceedings of the National Academy of the United States of America*** **[2021].**

For their study, Smith and colleagues provided twelve colonies of *Apis mellifera ligustica* with wooden frames that did not contain any foundation or wire supports. This allowed the workers to choose where, how much, and what type of comb to build (Photo 1). Comb was built on 23 of the frames over a period of 19 days, then the frames were removed from the colonies and high-resolution photos were taken of each comb.

Three general areas of interest were identified on each comb: "perfect comb," "transitions," and "merging." "Perfect comb" was defined as areas of repeated worker- or drone-sized cells that were not near frame edges, transitions, or merging areas. "Transitions" were defined as locations where workers transitioned from building worker-sized cells to drone-sized cells. "Merging" areas were defined as locations where workers merged two pieces of comb into one.

Next, automated image analysis was used for every cell in every comb to determine wall lengths, wall-to-wall length, interior cell angles, cell areas, and cell tilt. This allowed the authors to assess how regular the cells

Michael Smith

Photo 1 *Comb created by honey bee workers in an empty frame over a period of 19 days. Note the three separate starting points that will need to be merged if comb construction continues on this frame.*

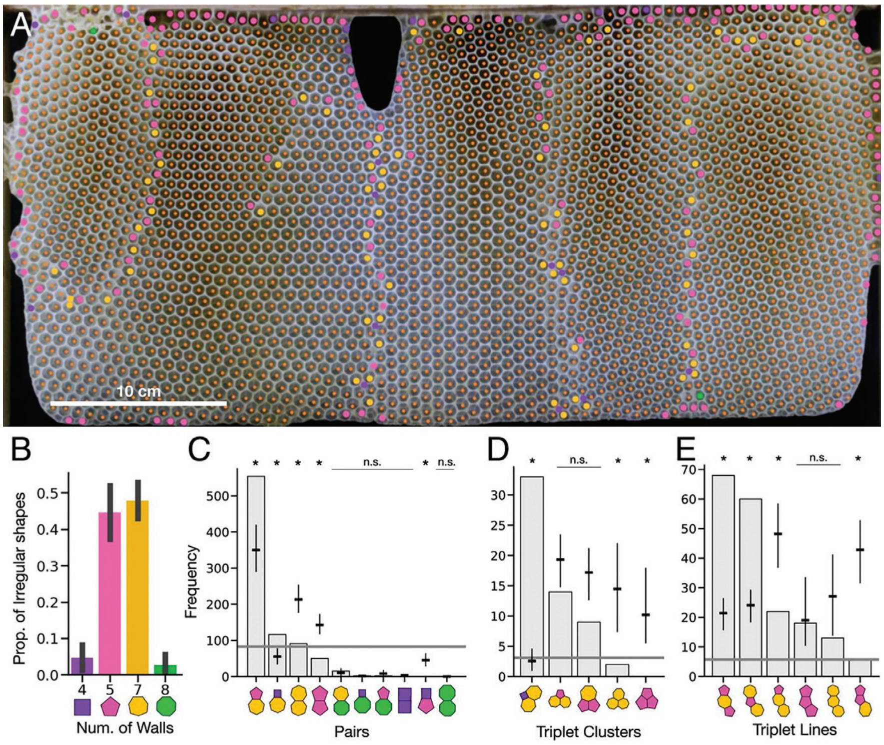

Fig. 1 *An example of honeycomb with cell centers marked and colored by number of walls (hexagons marked with small orange dots). Note in* **A** *that the analysis does not include cells within 20 mm of the outer perimeter due to image distortion and edge effects.* **B** *indicates the proportion of irregular-shaped cells, across comb transitions and merging (black bars denote 95% Confidence Interval). Frequency of irregular-shape pairs (***C***), triplet clusters (***D***), and triplet lines (***E***). In* **C** *through* **E***, the black dashes show the expected incidence when each cell type is picked independently according to its frequency of occurrence, while their vertical error bars show the full range of expected incidences following 10,000 random samples, with replacement. The gray horizontal line shows expected incidence for a uniform distribution.*

were in "perfect comb," and to assess how irregular the cells were in "transitions" and "merges." To test whether workers built combinations of irregular cells ("motifs"), the authors compared observed vs. expected incidence of irregular pairs and triplets based on chance. Finally, to test whether "merging" occurred haphazardly or by integrating information across multiple cells, Smith and colleagues developed two competing mathematical models from the perspective of merging two, perfectly regular, hexagonal tilings. One model was purely local and did not attempt to construct any nonideal cells, while the other model used global optimization to find a complete covering of space over multiple cells with possibly deformed cells.

So, what did they find? How perfect was "perfect comb"? Cells in "perfect comb" were highly consistent, which shouldn't surprise anyone who's taken a good, long look at comb before. For anyone who's wondering, after measuring 4,414 worker cells, the authors found that cell area = 25.7 ± 0.9 mm^2, wall length = 3.2 ± 0.1 mm, wall-to-wall length = 5.4 ± 0.2 mm, and cell angles = 120.0 ± 2.5°. By measuring 2,586 drone cells, it was found that cell area = cell area 37.5 ± 1.5 mm^2, wall length 3.8 ± 0.2 mm, wall-to-wall length 6.6 ± 0.2 mm, and cell angles 120.0 ± 3.2°.

What about transitions? Was cell size and/or shape adjusted during construction? Yes and yes. To transition between worker- and drone-comb, or to merge comb within the same plane, workers either built intermediate-sized cells or cells with irregular shapes as they approached the transition. As seen in Figure 1a-b, 4.4% of cells were nonhexagonal during comb transition/merging. Most of the irregular cells were 5- and 7-side, with 4- and 8-sided cells being less frequent (Figure 1B).

Interestingly, Smith and colleagues found a high frequency of 5-7 and 4-7 pairs and certain triplet combinations, such as 4-7-7 triplet clusters and sequences of 5-7-5 and 7-5-7 sided cells (Figure 1C-E). This shows that bees not only have a preference for certain types of irregular shapes, but also combinations of those irregular shapes. This same motif — pentagons paired with heptagons — is found in graphene grain boundaries, where two sheets of hexagonal carbon lattice are merged. In graphene, these defects are known to increase the material's strength. Whether the same benefit exists for honeycomb is unknown, but it's certainly intriguing to ponder!

What about merging combs that have different tilt? The authors found that the difficulty in merging comb also depends on the cell's relative position and tilt (Photo 2). As the difference in cell tilt increased at the merge, so too did the proportion of nonhexagonal cells. At its most extreme, over 60% of cells at the merge line were nonhexagonal.

So, is there evidence that honey bees are architects? To get a better sense for the extent to which worker building behavior involved complex global decisions (e.g., decisions that architects must make), Smith and colleagues compared the bees' merging strategies to two models. First, a "naïve model" where only hexagonal cells are built but are allowed to overlap at the merge line by a small area (Figure 2A-B). Second, a "global model" where hexagons are built until they reach the merge line without overlap, then the leftover space is filled with cell shapes that optimize space and position (Figure 2A,C).

The results show that honey bee workers outperform the naïve model by using irregular cell shapes, sizes, and tilts, but they underperform relative to the global model, probably because they have to optimize cells within constrained geometries. Overall, when faced with building tasks more complex than simple repetitive hexagons, both the global model and the bees arrived at similar strategies, including intermediate-sized cells and motifs of irregular shapes. In other words, there is definitely some support for honey bees building comb like architects.

Some researchers have suggested previously that honey bees are given too much credit for comb architecture — that in reality, they build round cells that assume a hexagonal shape when compressed together, ala the soap bubble effect. The idea of hexagons arising from circles pressed together originated from Pirk et al. (2004). A key to this idea is that honey bees heat themselves up to a point where wax flows and makes the hexagon through liquid equilibrium, like

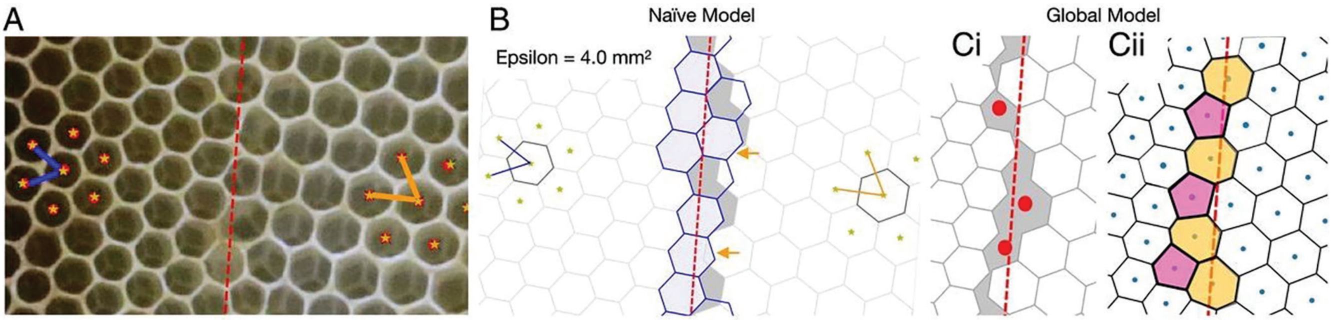

Fig. 2 *Example of a merge line (red) between worker (Left) and drone (Right) cells. The dots mark cell centers, and the lines mark the basis vectors for each coordinate system used for hexagonal tiling (***A***). Illustration of the naïve model, with blue cells tiled from the Left side toward the merge line. The blue-shaded cells are added (some overlap up to epsilon permitted, indicated by orange arrows), cells outlined in blue are not added, and gray shading marks unused space (***B***). Illustration of the global model, with red dots indicating added cell centers based on leftover area after hexagonal tiling (***C, i***). Output from the model based on the cell centers (blue dots), with five-sided cells shaded in pink and seven-sided cells in yellow (***C, ii***).*

soap bubbles. While very intriguing, the liquid equilibrium hypothesis was not supported in a later study by Bauer and Bienefeld (2013). Another important point is that even if hexagons formed like soap bubbles, the bees would still need to position the circles in a way that would nicely stack the cells.

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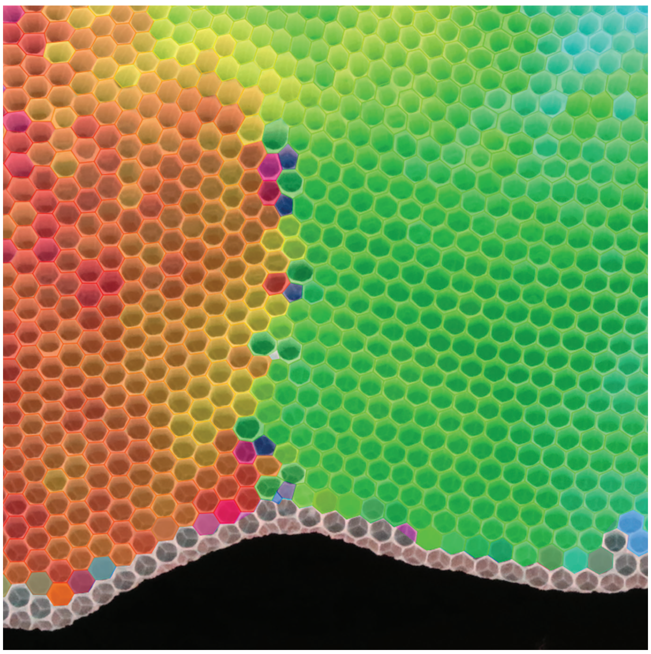

Photo 2 *Merging of two combs colored by cell orientation. Note the incidence of irregular shapes at the merge.*

As I sit in my living room and admire a 3-story castle built out of Legos by my 8-yr-old, I can't help but wonder how her placement of blocks would perform against a global model assessing architectural ability, or how it stacks up against comb built by bees.

Until next time, bee well and do good work.

Scott McArt

Reference:

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Pirk, C. W., H. R. Hepburn, S.E. Radloff and J. Tautz. 2004. Honeybee combs: construction through a liquid equilibrium process? *Naturwissenschaften* 91:350-353. **https://doi.org/10.1007/s00114-004-0539-3**

Smith, M. L, N. Napp and K. H. Petersen. 2021. Imperfect comb construction reveals the architectural abilities of honeybees. Proceedings of the National Academy of Sciences 118(31):e2103605118. **https://doi.org/10.1073/pnas.2103605118**

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