



Mechanical hive mind

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Honeybees work together to maintain a stable structure that adapts to environmental changes.

How do small animals buffer themselves against large fluctuations in their environment? One strategy is to form a superorganism, wherein individuals group together to overcome challenges a single organism cannot. Spectacular examples abound, and the behavior is a hallmark of social insects, such as termites, ants, and bees (see the Quick Study by John W. M. Bush and David L. Hu, *PHYSICS TODAY*, June 2010, page 62). This Quick Study focuses on the collective behavior of honeybees and describes how they stay warm and safe during their migrations to new nest sites.

At times, thousands of bees hold onto each other to create suspended clusters that can dynamically change shape to withstand mechanical stresses and regulate their bulk temperature. The stability of a cluster relies on individual bees that respond to local variations in strain. That behavior, in turn, improves the collective stability of the cluster as a whole, at the expense of increasing the mechanical burden experienced by individuals.

Collective behavior

The behavior isn't unique to honeybees. An individual organism—a bacterium, an insect, or a mammal, for instance—promotes the group's survival by sensing and responding to information from its local environment. A classic example is the positions of neighboring individuals in the group. That local information animates schools of fish and flocks of birds and allows them to collectively change direction abruptly and avoid predators. Similarly, collective decision making allows groups to locate food sources: Bacteria produce and detect chemical gradients, ants lay and detect pheromone trails, and bees use waggle dances to communicate and promote foraging.

Another process, also mediated via local information, is collective construction. It allows individuals to use materials from their natural habitat to build elaborate structures that are significantly larger than the size of an individual. Paper-wasp nests and termite mounds are two cases in point. Another type of collective construction is structures produced by individuals linking their bodies. Penguin colonies huddle together to stay warm in Antarctica, ants link their bodies to make bridges and rafts so they can traverse rough terrain and survive floods, and, as we'll see, clusters of honeybees have their own adaptations to keep their colony coherent and protected from environmental threats.

Honeybee colonies

European honeybees, *Apis mellifera* Linnaeus, reproduce via the queen laying eggs, and colonies reproduce via fission, a process

in which the colony divides roughly in half. The new colony is the swarm that leaves in search of a new permanent location while the rest of the bees remain behind. During that effort, the bees temporarily form themselves into a cluster that can hang from various surfaces—tree branches, roofs, and even fences and cars. It can also remain in place for several days while scout bees search the surrounding area for suitable nest sites.

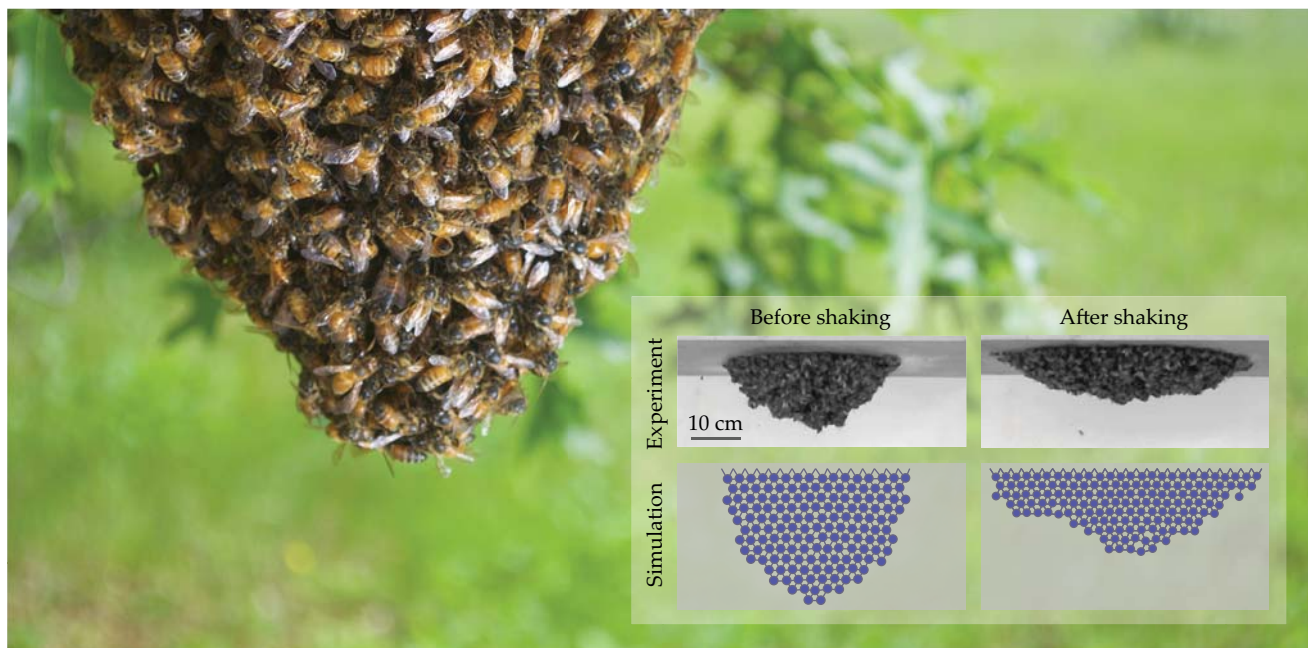
But the honeybees are still vulnerable. While suspended, the colony has no nest to protect itself from the elements. To cope with the exposure, clusters adjust their density and surface-to-volume ratio to maintain a near-constant core temperature—roughly 35 °C—despite large fluctuations in the ambient temperature. To generate metabolic heat, bees repeatedly contract and relax their flight muscles; to cool down, they ventilate the cluster by spreading out to increase the exposed surface of the swarm. Generally, a cluster takes the shape of an inverted cone, but the competing effects of gravity and mechanical perturbations of wind and rain produce a dynamic shape.

Morphology in motion

How can such a cluster, which is orders of magnitude larger than an individual, maintain mechanical stability in the face of environmental perturbations? My colleagues Jacob Peters, Mary Salcedo, and L. Mahadevan (all at Harvard University) and I addressed that question last year by performing a series of biological experiments and comparing the results with our computational models. Mechanical cues should play an essential part in the cluster's morphogenesis, we reasoned. To test the idea, we watched what happened when a cluster of approximately 10 000 bees was mechanically shaken.

The cluster was attached to a wooden board that oscillated along the horizontal or vertical axis at different frequencies (0.5–5 Hz) and accelerations (0.01–0.075 g). In response to the horizontal shaking, the conical cluster swung to and fro in a pendular mode, with a frequency of about 1 Hz. The bees dynamically adjusted the aspect ratio of their cluster and became, within minutes, a wider, more stable cone, as shown in the figure. As the frequency of the shaking increased, so did the forces on individuals, and they collectively widened the base of the cone to compensate. Its height shortened as a result. Once the horizontal perturbations ceased, the cluster reverted to its original shape, albeit at a slower rate than the bees took to flatten it.

When the motion was predominantly vertical, though, the shape remained constant until a critical force was reached that cracked the bonds between individual bees and caused the swarm to break apart. To understand the directional dependency in the cluster's response to motion, we modeled the clus-



A HANGING CLUSTER OF HONEYBEES changes its shape to improve the collective stability of the hive. Inset shows the experimental shapes and simulations of the cluster in equilibrium before and after horizontal shaking. (Images courtesy of Orit Peleg and Jacob M. Peters. For videos of the dynamic motion of a cluster, see O. Peleg et al., *Nat. Phys.* **14**, 1193, 2018.)

ter as an elastic material in which bees are represented by spheres connected to each other through elastic bonds. We monitored the mechanical strains on the bonds between pairs of bees and noticed that they are lower during vertical shaking than during horizontal shaking.

A positive correlation between swarm spreading and local mechanical strains suggests that the bees are monitoring those strains, not the global acceleration of the mechanical shaking. Moreover, the mechanical strains are lower when the cluster is spread out than when it is elongated. Apparently, the bees interpret low local mechanical strains as a cue to stop spreading.

The last component needed to reproduce the cluster's spreading is a directional bias. To that end, we monitored the spatial distribution of the strain inside the cluster and noticed that the strain decreases with distance from the attachment board. We combined all those ingredients into an agent-based model in which the bees monitor local strains and crawl up the strain gradient when those strains exceed a specific threshold. That response improves the collective stability of the cluster as a whole, at the expense of greater average mechanical burden experienced by the individual bees. One might call the behavior mechanical altruism.

Our model reproduced our experimental results: outward spreading in response to horizontal shaking and no spreading in response to vertical shaking. Because the spreading is a collective process, we wondered just how the bees pull it off. To study that aspect of the problem, we tracked the movements of bees on the surface of a spreading cluster. A change in relative displacement between neighboring bees drives the shape adaptation: Individual bees sense the local deformation of the cluster relative to their neighbors and move to regions of lower displacement.

In the continuum limit, that movement corresponds to the bees' ability to sense strain gradients and move from regions of lower strain (near the cluster's tip) toward regions of higher strain (near the fixed base). Importantly, that behavioral law is invariant to rigid translation of the cluster and depends only on the mechanical environment each bee experiences.

Our work has expanded the traditional understanding of collective behavior via stigmergy, whereby organisms respond to local cues with little or no long-range effects. The behavioral response of bees in the swarm is a new, previously unreported way to establish the relation between long-range elasticity and beneficial nonlocal effects mediated by physics.

Nonlocal interactions in assemblages of social insects may be the tip of an iceberg of ways in which organisms take advantage of physical interactions and simple behavioral rules for adapting to changing mechanical environments. As a broadly trained physicist studying animal behavior, I am fascinated by those painstakingly evolved solutions because they reveal new, optimal types of signal processing. By harnessing those natural solutions, honed by eons of evolution, we not only understand collective animal behavior more deeply, but we can also leverage the understanding to create bioinspired designs in the fields of dynamic construction, swarm robotics, and distributed communication.

Additional resources

- O. Peleg et al., "Collective mechanical adaptation of honeybee swarms," *Nat. Phys.* **14**, 1193 (2018).
- B. Heinrich, "The mechanisms and energetics of honeybee swarm temperature regulation," *J. Exp. Biol.* **91**, 25 (1981).
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- G. Kastberger, E. Schmelzer, I. Kranner, "Social waves in giant honey bees repel hornets," *PLOS One* **3**, e3141 (2008).
- T. D. Seeley, *Honeybee Democracy*, Princeton U. Press (2010).
- D. J. T. Sumpter, *Collective Animal Behavior*, Princeton U. Press (2010).

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