Swarm Intelligence:
How Tom Seeley Discovered Ways That Bee Colonies Make Decisions
Part II
by M.E.A. McNeil

A quest into the behavior of honey bee swarms is told in a new book destined to become a classic.

In the mirror where we see nature as a reflection of ourselves, bees have been loyal subjects to kings, socialist utopians, oracles. Scientific observation has looked behind that mirror to reveal unique creatures with fascinating behavior. Tom Seeley’s new book, *Honeybee Democracy,* looks at bees and humans through a two-way mirror, and the reader won’t see either quite the same way again.

Seeley is a professor at Cornell University, an entomologist and an ethologist – a scientist who values observation in the field over the lab and sees humans as not separate from nature. This mindset goes back to Karl von Frisch, who first deciphered the bee dance. His student Martin Lindauer discovered that an optimal nesting site for a swarm is chosen in a decision-making process by dancing scout bees. What intrigued Seeley was that it was a collective act – swarm intelligence a phenomenon mused over enough to go by its initials, SI. The story warrants a synopsis: In 1974, the summer before he started graduate school at Harvard, Seeley set up an artificial swarm and a nearby nest box. “The scout bees chose my humble plywood box for their future home. Soon I was dashing back and forth along the 150-meter-long (500’) path between swarm cluster and nest box doing my best to watch both the growing party of excited dancers on the swarm and the strengthening throng of scout bees scrutinizing the nest box.” Quite suddenly, he wrote, he found his box, which had hosted 25 scouts, deserted. He looked back to see his swarm, “a diffuse ball of swirling and shining bees rolling straight toward me over the sunny field”. How did that happen?

In 20 years nobody had solved the mysteries raised by Lindauer's work. “I decided simply to watch, with my eyes wide open, a swarm go through its democratic decision-making process,” wrote Seeley. This book is the engrossing story of the revelations that followed.

His quest unfolds with focus, but there was little to guide Seeley, who said that he started, “picking up where Lindauer left off, then just following my nose. ‘Okay, I've seen that, documented that, and that -- well that was curious’. I didn't have a grand plan.” Most importantly, he said, “I paid attention to the surprises.”

He knew, from Lindauer, that swarm scouts are forager bees. That made sense because they are the only bees with an orientation to both the outside environment and the colony inside the hive. These recast foragers somehow get the swarm to the best home. Because he could “accurately think of the honeybee colony as a single living entity,” he was looking for the relationship between the behavior of individual scouts and the whole.

To begin with, what were they looking for? To understand what the criteria might be, he assessed the nest cavities of feral bee colonies. Foremost among several requirements, he found,
was size: large enough for brood and stores to survive the winter and small enough to heat efficiently -- approximately 40 liters (about 10 gallons).

A small island off the coast of Maine called Appledore was an ideal place to test swarm behavior, since there were neither honey bees nor nesting sites there. It is Seeley’s process that makes such wonderful reading: “Putting a spot of paint on the thorax of different bees transformed them from mere members of *Apis mellifera* into personal acquaintances whose affairs became of the greatest interest to me.” And to the reader, too.

Each study is ingeniously devised. “Tom is a master at designing experiments in the field,” said entomologist Mark W. Moffett, a researcher at the Smithsonian Institution. Seeley’s observations, intriguingly described in the book and touched on in Part I of this article, revealed how the scouts explore the qualities of a potential home -- cavity volume, entrance height, entrance size, presence of combs from an earlier colony – and how they report their findings.

“A colony achieves near-perfect accuracy when it selects its home. It is a life or death matter,” he said. But the questions remained: How do the bees make a decision? And then, how do they then fly toward a site so few have seen?

Between Seeley and the answers was the cost to film this process, which was prohibitive in 1975. So he made an educated detour, spending the next 15 years studying behavior that he suspected was another manifestation of SI: colonies deciding how to distribute their foragers among flower patches. He documented how bees make collective decisions by communicating floral sources on a “bulletin board of job opportunities”. He knew that foraging and house hunting had to be related in some way: “I didn't understand the similarities at the time. I proceeded from a gut sense...In hindsight it's quite clear,” he said.

When Seeley turned from his foraging studies to investigate swarms again on Appledore Island, he had more pieces of the SI puzzle in place, and that would serve him well. Choosing a home, though, is a different sort of collective
choice: It is an ephemeral phenomenon that lasts at most a few days, whereas foraging goes on all summer long. Generations of foragers could pass without the need for swarm scouts, and then, he wrote, some “radically switch their behavior. Instead of seeking bright blossoms, they search for dark crevices.”

Where to begin to understand? “You start with the question. You start observing. Let the bees be your guide,” said Seeley. He now had camera equipment that had become both more sophisticated and less expensive. He could use slow motion playback to create a record of the scout bees’ dance activity. To keep track of the dramatis personae, he needed to label the bees. He’d picked up the skill in his foraging studies and could mark 100 in an hour. But even for the small swarms that he created – half to a quarter the size of a normal swarm – it would take 40 hours to mark each colony.

The camera needed to be tended for the two days it took a swarm to choose a new home. Then the information had to be slowly extracted from the footage -- identifying each scout, the indicated location and number of circuits of all of her dances, the beginning and ending of her search. It was a formidable amount of painstaking labor. Seeley called it “his immense good fortune to be joined by Susannah Buhrman, a bright Cornell undergraduate,” who documented the swarms with him. They watched scouts dance for multiple sites and observed a growing unanimity, after which the swarm flew off in the decided direction. The prevail, with the ante as high as a triple scoop ice cream cone. When the bees departed, the humans made a bee line for the ice cream store.

Each 16 hour film of the bees’ decision-making process took Buhrman a month to decipher. The summer of 1997 produced a complete record of the dances performed for three swarms. The resulting diagrams showed the scouts searching something 70 km² (about 30 mi²), starting slowly and adding widely scattered alternatives. Most sites were reported during the first half of the decision-making
period, but sometimes an ideal location was found late in the discussion. Each scout reported several times, but always on the same site.

Making this task marginally less than impossible is that the number of scouts is proportionately few: in the three small study swarms, 73, 47, and 149, but in a natural swarm 300 to 500. And all of the activity is on the outer layer of the cluster where it can be observed.

“After a while your eye develops a search image -- you get pretty good at spying the dancing bees,” said Seeley. “When you've got these bees individually labeled, you realize that they're not all the same, not cookie-cutter. They've got their little quirks to them. Some are really good dancers, some are not very good dancers, some are really peppy and get going really early in the morning, and some have to be woken up. There's a lot of personality, I might even say.”

The statistics revealed patterns: Each scout bee visited one site several times, but the number of dance circuits she made declined each time she returned. Eventually, each scout would leave the search to sequential waves of new scouts -- creating multiple independent reports.

The pattern of dances for eleven possible nest sites, observed by Buhrman and Seeley in July, 1997, involved a prolonged competition between various sites. From Hive Democracy by Thomas Seeley.
“I suspected a lot of things that turned out to be incorrect,” said Seeley. “I suspected that this was a consensus building process, because that's what you see … But we were surprised to find out that the scouts themselves don't pay any attention to whether or not they have a consensus. They pay attention to whether or not they've got a quorum for one of the sites.” That quorum is 20 to 30 bees present simultaneously at a potential nest – representing reports from many more retired scout bees.

A good conclusion arrives with a new question for Seeley: Why don't the scouts use consensus sensing? He teamed up with Kevin Passino, a professor of computer engineering specializing in biomimicry at Ohio State University, to create a computer model of the process of nest site selection. They adjusted the quorum down to 15 bees present at a virtual site, which resulted in quick but error-prone decisions by the game bees. Increasing the number above 20 to 30 bees produced slower but only slightly better decisions.

The simulation showed that the bees set the quorum high enough to make accurate decisions and low enough to save on the duration of their exposure and resources. A longer process could mean another cold night out, which would diminish their small fuel reserves and produce little or no improvement in the result.

How does this search committee comprising fewer than 5% of the bees move the swarm to its new home? The scouts began with an auditory signal, a worker piping. “It's a little sound like zzt, zzt,” said Seeley, who offered the following suggestion to an incredulous public audience: “Next time you have a swarm…and you are watching it, if you put your ear up next to it, shortly before the swarm takes off to fly away, you'll hear that piping sound, it's actually audible to the human ear.” The non-beekeepers gasped at the audacity of the thought; the beekeepers, knowing a swarm to be harmless, could be indentified by their chuckles.

Seeley’s curiosity about what triggered the sound was shared by Kirk Visscher, an inventor, statistician, computer whiz and entomologist on the faculty of the University of California at Riverside. They experimented on Appledore Island in 2002 and 2003 and concluded that reaching a quorum at a proposed nesting site is the stimulus for piping. And what purpose does the piping serve?

They discovered that coincident with piping, the bees warm up their flight muscles in preparation for leaving. Bees fly with wings moving some 250 times per second, requiring their wing muscles to be very warm -- 35° C (95° F). To raise the temperature, they disengage the thoracic muscles from their wings and vibrate them. Getting the whole swarm up to flying warmth takes about half an hour, with the pipers moving inside the hanging swarm and then along the surface, signaling.

Bees on the surface of a swarm photographed by an infrared video camera. Left: 15 minutes before takeoff. Right: 1 minute before takeoff. The scale bar is in Celsius, measuring from about 77°F from the darkest to about 106° F to the lightest. From Honeybee Democracy by Thomas Seeley.
Worker piping coincides perfectly with swarm warming and takeoff; the pitch of piping even matches the beat frequency of a flying bee. But Seeley puts on his scientific brakes: correlation is not the same as causation. It was simply a hypothesis until he tested it with Jürgen Tautz, an inventive bee expert at Wurzburg University in Germany. Scouts were prevented from sending piping signals to half a swarm by means of a special cage. The other half showed the usual pattern of warming and taking off. The caged bees proved too cold to fly, not having gotten the signal to prepare their flight muscles.

Lindauer reported another behavior in the final few minutes before a swarm departed, which he did not understand – bees running across the cluster with outspread wings and buzzing noisily. His questions had lingered for over half a century about this phenomenon, called the buzz run: “What is the interplay between worker piping and buzz running as the swarm prepares for flight? Which bees in a swarm perform buzz runs? How do buzz runners know when to produce their signal?”

Seeley set up another painstaking film surveillance with the assistance of Cornell undergraduate student Clare Rittschof. It began when the scouts started piping and ended when the bees left for their chosen home. The recordings were played back in slow motion and scanned by Rittschof for bees running in an imitation of flight. She saw them buzzing over and between docile bees, stirring them to move. More and more bees were found buzz running during the final hour before takeoff. Almost all of them made the pipers, who were already known to be scout bees.

Each of two scouts dances for a site, one with a larger opening and one with a more defensible, therefore more desirable, smaller one. The blue diagrams show the number of dances performed by the two scouts, with the better space danced more frequently and attracting more bees. Illustration modified from T.D. Seeley, P.K. Visscher, and K.M. Passino, American Scientist, 2006.
Ritualization is the name biologists have given to the process whereby a behavior becomes modified into an intentional signal. In this case, the buzz run is a flight-like demonstration that stimulates other bees to take to the air.

It is the piping scout bees that can tell when all of the bees in the swarm cluster are warm enough to fly. The buzz run signal shares this information group activators,” wrote Seeley. The surface of the swarm is the last to warm up and, “right when it gets to that temperature, boom, the thing lifts off,” he said.

How does the swarm fly so decisively to a destination that fewer than 5% of the bees in the swarm have seen? Seeley and Kirk Visscher plotted swarm flight speeds on Appledore Island, dodging thickets of poison ivy. They observed the bees hovering over their bivouac site for half a minute or so and then starting slowly, at less than 1 km/hr (about ½ mi/hr) toward the nest. They accelerated to 8 km/hr (5 mi/hr) until stopping near the goal – where scouts fanned Nasonov pheromones to guide the others to the opening. Within ten minutes of arriving, all the bees were safe inside.

The process of winnowing down three hypotheses to explain this behavior is well worth the read. In 2004, Seeley had been joined by Madeleine Beekman, a behavioral biologist from the Netherlands. To test whether the bees follow a chemical signal, they devised an assiduous method of sealing the Nasonov glands in each bee of a small swarm. The bees had no problem flying to the nest site, proving that they did not follow a pheromone. They did, however, find it more difficult to locate the entrance without scent markers.

Two more hypotheses had been advanced: the scouts could be either “subtle guides” that nudge the swarm along or “streaker bees” that repeatedly shoot toward the goal, which was Lindauer’s guess. Beekman and Seeley looked for “streakers” with slow film and were able to capture a pattern of a few bees blazing across the top of a moving swarm.

By 2006, Kevin Passino was on the cutting edge of point-tracking algorithms in computer vision. He joined Seeley and Kirk Visscher on Appledore Island with a highdefinition video camera to record an airborne swarm from below. Three-dimensional reconstructions of the individual bees’ flights were made over the next two years by Passino’s graduate student Kevin Schultz. The “streaker bee” hypothesis prevailed, but not before swarm chasing adventures and analytical explorations that are page turning reading.

In discussing his work with his colleagues in the Cornell Department of Neurobiology and Behavior, Seeley was surprised to learn that a swarm of bees functions much the same way as the primate brain. It made sense: each scout reports on a single find, much like each neuron in the brain fires in response to a particular stimulus. “Both are cognitive entities that have been
shaped by natural selection to be skilled at acquiring and processing information to make
decisions,” he writes. In both systems, an accumulation of input surpasses a critical threshold
that signals a definition/decision.

“I like to think of the swarm as a kind of
exposed brain that hangs quietly from a tree
branch but it’s able to ‘see’ many potential nest
sites spread over a vast expanse of the
surrounding countryside. As we have seen what
gives a swarm such an immense ‘visual field’ is
its squadron of several hundred scout bees.”

Seeley took the comparison another step.
Although SI has been investigated mostly in
social insects, he saw relevance to the behavior
of other animals, including humans. Science, he
says, can be thought of as a kind of collective
wisdom, with multiple reports of particular
experiences forming a kind of quorum – with, for
example, dances for the round earth theory
trumping those for the earth as flat.

He posits that we can learn collective
decision making from the bees. Their lessons can
apply where people meet with a common goal in
what is called unitary democracy -- such as a
New England town meeting.

“For fun, and as an experiment, I decided
to introduce some of the ways the scout bees go
about choosing a home to the ways my fellow
professors and I hold deliberations in our monthly faculty meetings,” wrote Seeley. From that
experience he describes “five habits of highly effective groups that I’ve learned from the bees”
– a sensible primer for group organization in another engaging chapter of the book.

In The Smart Swarm, a book inspired by Seeley’s work, Peter Miller describes some
people in an audience starting a standing ovation with others feeling compelled to join a
consensus, regardless of their individual opinions of the speaker. He makes the point that bees
behave differently; they come to a group decision by acting independently. Seeley writes, “The
bees have something to teach us about building smoothly functioning groups, especially ones
capable of exploiting fully the power of democratic decision-making.”

After Honeybee Democracy was published, Seeley looked back on the experience: “The
most surprising thing that I learned in all this is just how behaviorally complex these bees are.
They can go out across the countryside, find a site, measure it, come back, report on it go back
out, measure a quorum, and if there is a quorum they switch from waggle dancing to piping,
then switch from piping to buzz running. This is all done by a little insect. That's really the
take-home message.”

“I don't think I would have understood or thought as carefully about the parallels
between brain decision-making and swarm decision-making if I hadn't taken the trouble to write
this book. And I also would not have thought about what I call “swarm smarts” -- what we can
take from the bees to improve our own group decision-making.
“It all makes sense in the end, but it doesn't all make sense initially. Sometimes you just have a hunch.”

Seeley’s educated intuition makes for a book filled with surprises, doubts, rich philosophy, decades of patient scientific discovery, camaraderie, and love for the bees.

“There are many questions left unanswered,” he said. Seeley has taught us to expect that when he answers the next ones, he will find more -- and we hope to come along on the expedition.

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3 Phone interview, 10-23-10.
4 Recorded interview, 10-6-10, The California Academy of Science. Quotes designated “said” come from this or the subsequent interview.
5 Lecture, The California Academy of Science, 10-6-10.