More Fun Than Fun: The South Asian Greater Banded Hornet Waits to be Studied

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Miriam Lehrer (1933-2005) in her office at the University of Zurich, perusing graphs showing the results of her experiments. Photo: M.V. Srinivasan

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This article is part of the 'More Fun Than Fun' column by Prof Raghavendra Gadagkar. He will explore interesting research papers or books and, while placing them in context, make them accessible to a wide readership.

I was recently excited to read a paper entitled "Visual associative learning and olfactory preferences of the greater banded hornet, *Vespa tropica*". It was published by my colleague Hema Somanathan and her students and collaborators at the Indian Institute of Science Education and Research (IISER), Thiruvananthapuram. The paper demonstrates that wasps learn to associate colour, shape and smell with a food reward.

There are many reasons why this paper especially aroused my interest. First, it is an excellent example of simple, clever and inexpensive experiments that I am so passionate about. Second, the study builds on the work of two of my heroes, Karl von Frisch and Miriam Lehrer. Third, the authors of this study have succeeded where my students and I have failed. Finally, the object of their research is a wasp species that I have tried hard to keep away from my laboratory with a significant expenditure of time and money!

Let me try to unscramble the multiple emotions aroused by this paper, and attempt a linear narrative.

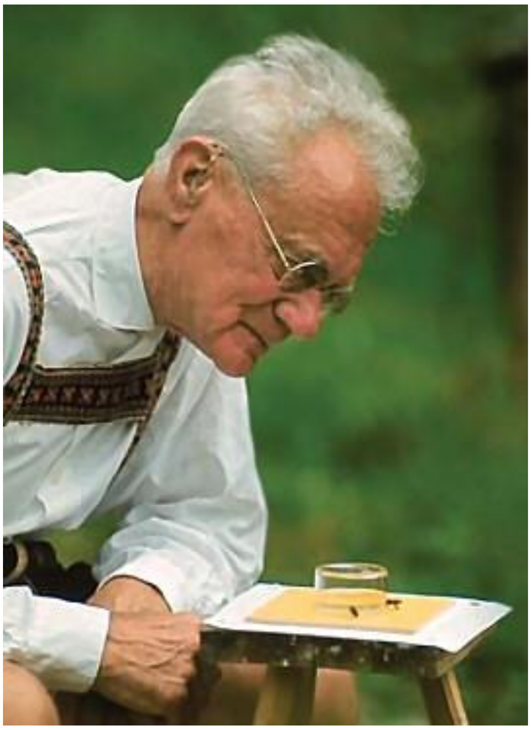
Do bees have colour vision?

Long before getting the Nobel Prize and long before doing his prize-winning work, the young Karl von Frisch asked a simple question: why are flowers so brightly coloured? The obvious answer seemed to be "to attract bees". But a distinguished scientist of his day, Richard C. von Hess, had apparently established that bees are colour-blind.

Finding his suspicion so compelling, von Frisch conducted his own experiments to test the idea. He trained honey bees to collect sugar solution from a container placed on a coloured cardboard in the garden. Honey bees sucked up the solution, stored it in their crop, flew back home, delivered the sugar solution to waiting unloader bees and returned for more. After the bees had made a few trips, he expected them to associate the colour of the cardboard with the food reward, provided they had colour vision and were good learners.

While the bees were away, von Frisch cleaned up the table and placed two fresh cardboards, one of the original colour familiar to the bees and another of a different colour not familiar to the bees. If the bees could distinguish between the two colours and remembered the colour that initially gave them the reward, they should now alight on the cardboard with the original colour. And that is what the bees did!

von Frisch realised, of course, that even if bees did not have colour vision, they might distinguish different colours that could be appearing to them as different shades of grey. He ruled out this possibility by showing that bees did not confuse the colour they had learned with any of the many shades of grey he presented them, before claiming that honey bees had colour vision.



The German zoologist training bees to collect sugar solution from a place of his choice. Photo: Author not known. Immediate source: https://en.wikipedia.org/w/index.php?curid=50796040, fair use

von Hess did not relent. The clash between von Hess and von Frisch is both poignant and instructive, and needs to be told and re-told. von Hess used his stamp of authority to claim:

> "It was possible to demonstrate that the claims of … von Frisch, according to which bees can be 'trained' to certain colors, are wrong altogether … not a single fact is known that could even make plausible the notion of a color sense in bees … through my investigations, this assumption is terminally refuted…"

This prompted the young von Frisch to write to his mother:

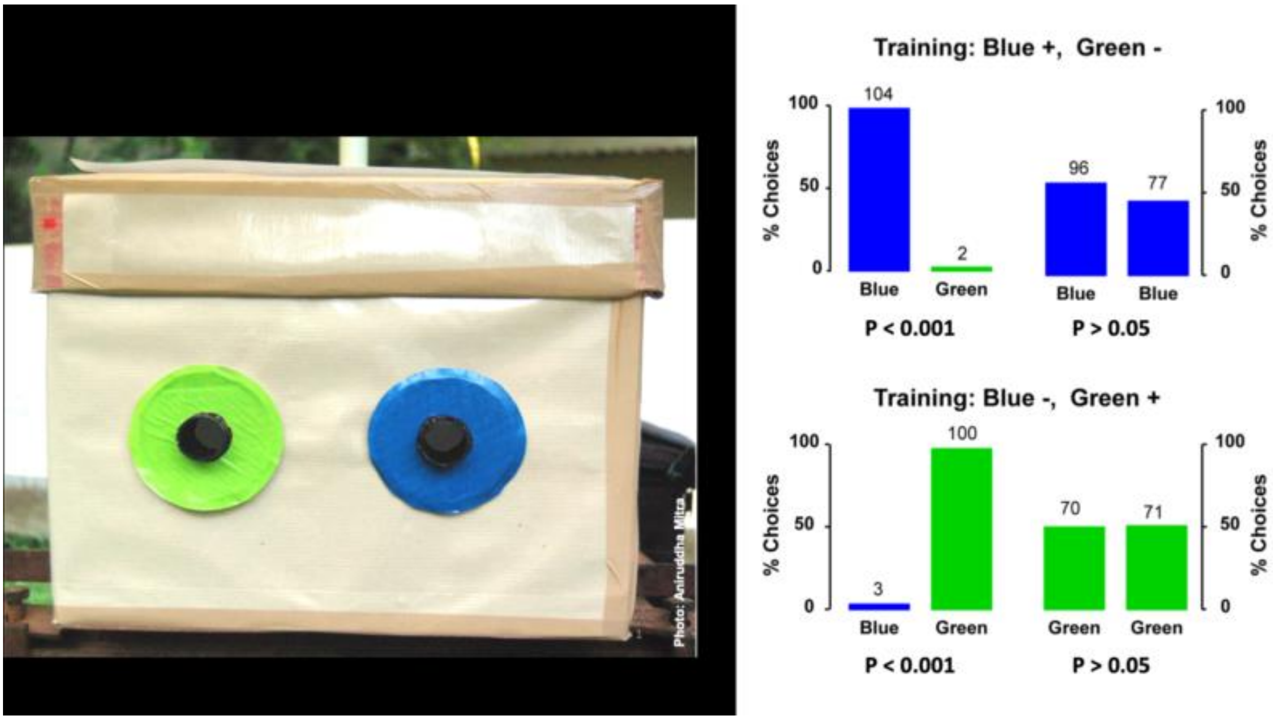
> "I have the uncomfortable feeling that I now have a real enemy in the world out there, the first one, and someone who could really damage me…"

Today, we know that von Frisch was absolutely right, we understand why von Hess came to the wrong conclusion, and we know much more. We know with certainty that bees have true colour vision – in fact, trichromatic colour-vision like humans. However, their spectral sensitivity is a bit shifted from ours: bees have cones tuned to UV, blue and green instead of red, blue and green, like us.

von Frisch's experiment is so simple and so clever that I have often encouraged high school students to repeat it with slight modifications. The students fabricated a cardboard box with two possible entrances using disks of two different colours, and some sugar solution inside the box. By closing one of the entrances, the bees could be trained to associate the reward of food with one but not the other colour.

In one experiment, the students trained the bees to enter through the blue entrance only, as the green entrance was kept closed. When tested later, the trained bees (marked for individual identification) entered through the blue entrance in 104 out of 106 trials. When trained to enter through the green entrance, they chose it correctly in 100 out of 103 trials.

The second experiment shows that it is not blue or green that they are fond of, but the food itself, and they remember how to get to it, colour and all. In a crucial control experiment, the students tested the trained bees by offering them discs of the same colour at *both* entrances. Now, the bees used both entrances equally, showing that it is not the left or right entrance that they had learned but the colour of the disc at the entrance (see the illustration).



Left: experimental cardboard box with two entrances with different coloured discs. Right: results of training bees, as explained in the text. Source: Author provided

Not content with merely repeating von Frisch's experiment, and notwithstanding his Nobel laureate status, my students went on to make innovative modifications to the original experiments. They demonstrated that bees could learn that while blue may be rewarding in the morning, green could be rewarding in the afternoon.

Another creative modification, made when M.V. Srinivasan and Shao Wu Zhang visited our lab, showed that bees could learn to choose one colour at the feeder and a different colour to enter their hive, switching their preference in seconds as they moved from one to the other. (You can read a fuller account of von Frisch's and my students' experiments in the second chapter of my free ebook, *Experiments in Animal Behaviour*.)

Miriam Lehrer

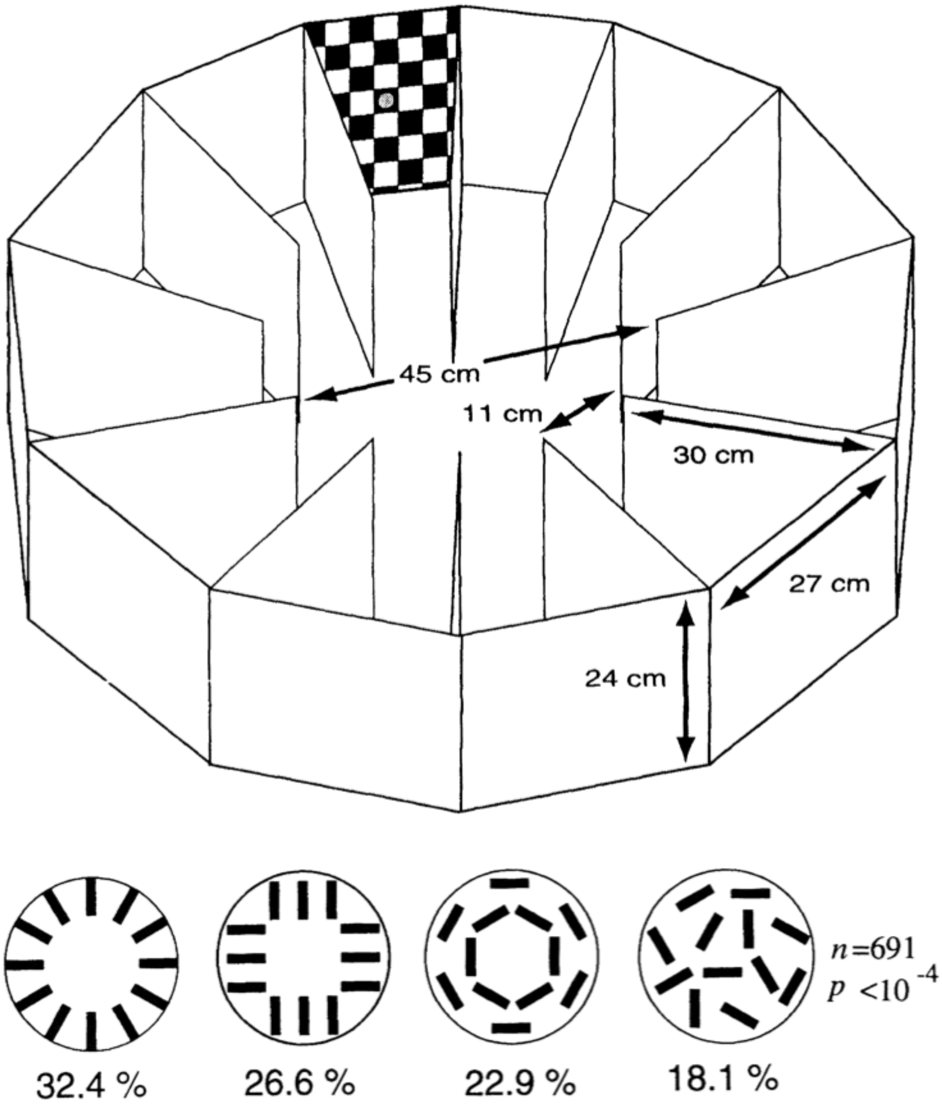
I first met Miriam Lehrer in 1992 on a visit to the University of Zurich. After my seminar at the Zoology Institute, Miriam gave me an hour-long private seminar on her fascinating work on shape and movement recognition in honey bees, including her then-most recent discovery of the "turn-back-and-look" behaviour, which later made her famous.

In a 1991 paper, Miriam had described her finding that when bees visit a new food source and are flying back home, they literally turn back and take a good look at the landmarks around the food so that they can return to it later without difficulty. Their turning back to look is quite deliberate, involving flying sideways repeatedly, to the left and to the right, while facing the food as it slowly disappears from her view.

I had the good fortune to meet Miriam again when our mutual friend M.V. Srinivasan invited me to spend a month at the Australian National University in Canberra. I was quite content to spend my time meeting and speaking to many famous scientists there and reading in their excellent library. But Miriam, who – unbeknownst to me – was also visiting Srinivasan, kindly invited me to participate in her ongoing experiment.

The aim was to see if bees had an innate preference for flower-like radial patterns. Her simple, elegant and inexpensive apparatus was an open plywood box with 12 compartments placed in the garden. Bees could fly into any compartment of their choice and go through a small opening to get a sugar reward. We placed the apparatus on a turntable and rotated it manually from time to time.

After the bees had learned the trick, we placed different patterns on the walls of each compartment and removed all rewards. The bees had learned that there is a reward in all compartments, but they could choose routes with different patterns to get to the reward. Now, the bees should reveal their innate preferences by entering the compartments of their choice (see image).



Top: A simple apparatus to test the innate preferences of bees. Bottom: examples of patterns offered.
Reprinted from Lehrer et al., Phil. Trans. R. Soc. London, 347, 123–137, 1995.

When offered different patterns, the bees showed a statistically significant preference to go through the compartment with patterns containing radial, flower-like symmetries instead of patterns with less or no symmetries.

Miriam did the lion's share of the work and saw this through publication. In hindsight, it is not surprising that bees have an innate preference for flower-like radial symmetry – they get all their food from flowers, after all. Miriam's strength was two-fold. First, she recognised that this was an important hypothesis, and that though obvious, it had not been properly tested before. Second, she found a simple and elegant way to test it.

I like to think that some of Miriam's love for simple and elegant experiments has rubbed off on me. Incidentally, Miriam worked on wasps, too.

I subsequently had the pleasure of hosting her in my laboratory at the Indian Institute of Science, Bangalore, in January 1995. As in her science, Miriam was also simple and elegant in her personality, and very modest. She told me nothing about herself, although there was so much to tell, as I learned after she passed away in August 2005.

Let me quote a few lines from a tribute to her by Srinivasan, published in the November 2005 edition of the International Society for Neuroethology newsletter.

> "Miriam was probably one of the most skilled and accomplished researchers of honeybee behavior in her time… Born in Poland, Miriam completed her schooling in Israel. She then took up a position in the Academic Corps of the Israeli Army, whilst concurrently matriculating in the field of Bacteriology at the Hebrew University. Marriage took her to Switzerland, where she spent her first twenty years raising a family in Zürich. In 1972, as a single mother of two children, she decided to resume her academic life. She enrolled in the University of Zürich and obtained an undergraduate, a Masters' and a Ph.D. degree in the faculty of Zoology, before taking up an academic position there in 1980. A golden period of research followed, and continued up to the very last day of her life, despite the devastating and untimely loss of her son in 1998."

Miriam's was a life worthy of celebration and emulation.

Miriam Lehrer training honey bees at a feeder with sucrose solution in the balcony of her office in the University of Zurich. Photo: M.V. Srinivasan

Central place foragers

Ants, bees and wasps are called central place foragers because a small number of specialist foragers scout the surrounding environment and transport food back to a central place – their nest. Because a few foragers gather food for all their sisters, which may number in the hundreds to hundreds of thousands, the foragers are highly motivated to search for food.

Not surprisingly, these social insects have been favourite models for understanding how animals learn the size, shape and colour of nectar-, pollen- of seed-bearing plants, and how they find their way about.

Although my students and I have worked on the Indian paper wasp (*Ropalidia marginata*) for four decades, and vowed to understand everything about them, I'm afraid we have not been successful in training the wasps with food rewards. Part of the problem is that our wasps are not very motivated to feed on what we give them. They seem to get better stuff on their own. Besides, their colonies are small, and their main food consists of other insects and spiders. Our failure is one reason I was excited to read the paper on the learning abilities of wasps that I mentioned in the beginning.

Yet another reason was, I must confess, the mention of *Vespa tropica*.

The hornet

The south Asian great banded hornet (*Vespa tropica*) is quite different from the Indian paper wasp, the primary study species in my laboratory. *Vespa tropica*, an invasive species in some parts of the world, builds large, enveloped nests with many layers of combs stacked on top of each other. Its colonies consist of a single large queen and thousands of workers. Their main food items appear to consist of honey bee adults and *R. marginata* larvae and pupae. For this reason, these wasps are a great nuisance for our work and for those who work with honey bees. *V. tropica* foragers regularly visit *R. marginata* colonies and devastate them. I estimate that *V. tropica* is mainly responsible for regulating the populations of *R. marginata*.

Images of a nest of the hornet Vespa tropica that I collected from the IISc campus, showing the intact nest (before collection) (left), the multiple layers of comb visible after removing the envelope (middle) and the fact of the combs studded with pupae (all adult wasps have been removed). Photo: R. Gadagkar lab

Our research on *R. marginata* has only become possible because we have (more or less) successfully kept *V. tropica* out of our lab. We have done so by constructing a vespiary covered with a wire mesh on all sides – the mesh size being small enough to keep most *V. tropica* wasps out but at the same time permit *R. marginata* wasps to fly in and out freely. The paucity of our knowledge of the sister species, *R. cyathiformis*, compared to that of *R. marginata* is mainly because of the inscrutable unwillingness of *R. cyathiformis* to thrive in the vespiary: they just leave and never return.

Perhaps we were so busy hating *V. tropica* and keeping it away that we never bothered to study it carefully!

Quite in contrast, it is this very habit of marauding their experimental honey bee colonies that led Hema Somanathan and her students to study it. Unlike us, they couldn't keep it away, so they decided to study it. Hema recounted their story thus:

> "My students Reshnu Raj, Jewel Johnson and Balamurali were running associative learning experiments using colour stimuli in honey bees on the rooftop of the lab building.
>
> To entice bees, we place a feeder close to the hive, which the bees eventually discover and then they can be trained by moving the feeder in small steps into the experimental arena. Soon, hornets would appear near the hive flying around, and then we expected them to start preying on bees – which we have seen them do – especially when returning foragers slow down as they approach the hives.
>
> The team would shoo the wasps away, but they kept coming persistently to the feeder to lap up the sucrose in it. We were quite amused to find them landing on the sucrose feeders and ignoring the bees. Sometimes prey and predator would feed side-by-side. But then we became impatient and annoyed that the bee numbers eventually declined, though there were a few brave bees that still persisted. Nothing would keep the hornets away.
>
> So then, we said, what the hell? Let's study them anyway while we wait for the bees. They behaved perfectly in our experiments, marked individuals would return regularly, and learnt in just 1-2 trials to associate colour or odour with a sucrose reward.
>
> Compared to bees, we found them much easier to work with, so we stopped complaining."

Vespa tropica wasps stealing the sugar solution kept for honey bees in the experiments of Hema Somanathan and her students, by themselves (left) and alongside honey bees (right). Photo: Hema Somanathan

By training the wasps to feed in specific situations, Hema and her students demonstrated that after only six sessions, the wasps learned to associate food reward with a particular colour (blue or green) and shape (square or triangle). Their experiments also demonstrated a phenomenon called colour generalisation. When the wasps appeared to make mistakes, they did not choose other colours randomly. Instead, they were more likely to choose colours that were perceptually more like the learned colour.

It is easy to see that such an ability to generalise, well known in honey bees, would come in handy to deal with natural variations in the colours of flowers that they have learned to be rewarding food sources.

From left: PhD student Balamurali, Hema Somanathan and integrated BSMS students Jewel Johnson (top) and Reshnu Raj. Photos: Hema Somanathan

The tyranny of novelty

These preliminary experiments (compared to what we know about honey bees) by a team from IISER Thiruvananthapuram, I am proud to say, suggest that *Vespa tropica* wasps offer an excellent model system to study the perceptual and learning capabilities of another social insect, and to make comparisons with honey bees.

I think biologists focus far too much of their research efforts on a few so-called model species, such as honey bees, for example. One reason for this is that we find it easier to make one or two incremental steps in a well-established chain of previous research. On the other hand, it is much harder to work on a relatively less-known new species and start from scratch – it takes courage. But a new species may yield unexpected new knowledge and advance our understanding much more in the long run. In the beginning, however, work on new species will sound less spectacular than cutting-edge work on a model species.

There is an inevitable trade-off between the safe option of working on a model species and the risk of working on a non-model species. Individual researchers should be free to make their choices depending on their own biases and their circumstances. But we should not disparage preliminary work on non-model organisms on the grounds that they lack novelty and the level of sophistication possible with model organisms.

I congratulate Hema Somanathan and her students for their courage in experimenting with a new, non-model species, and I am delighted to see that my favourite journal, *Insectes Sociaux*, has had the wisdom to publish their 'preliminary' work.

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