More Fun Than Fun: Chasing Wasps on a Bicycle – and Getting a PhD

26/05/2021

Souvik Mandal chasing wasps on his bicycle in the IISc campus to discover how they find the way back to their nest. Photo: Souvik Mandal

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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 confess to having been in love with the Indian paper wasp (*Ropalidia marginata*) for over 50 years. For almost 40 of these 50 years, it has also been the sole object of my scientific research, much of which I have pursued in collaboration with a large number of students, equally passionate to probe the mysteries of this amazing insect society.

Female wasps scrape cellulose fibres from the surrounding vegetation to manufacture paper and construct honeycomb-like nests. One of the female wasps in the colony assumes the role of the queen and lays eggs in the hexagonal cells. The remaining female wasps function as non-reproducing workers. They cooperatively build and repair the nest, clean and defend it from parasites and predators, including other wasps of their own species. Older wasps also venture outside the nest to hunt for soft-bodied insects and spiders, which they bring back to the nest and share with their adult nestmates and feed to the growing larvae. They are called foragers.

Like any insect society, the wasps display impressive levels of communication, coordination and division of labour. They appear to tread a delicate balance between cooperation and conflict, especially because workers can potentially overthrow their queens and take over their role of leave to start their own new nests, often taking a small number of loyal followers with them.

Not surprisingly, sitting in front of a nest, with the wasps marked with coloured paint spots for individual identification, can be the source of endless pleasure and innumerable opportunities to probe the evolutionary logic behind every behaviour of the wasps.

A relatively large nest of the Indian paper wasp Ropalidia marginata, with all wasps marked for individual identification. Many larvae and pupae can also be seen as many wasps seem to sit a little away from the nest temporarily.

The quest for understanding the behaviour of the wasps is endless, and it is so much fun and so easy to watch the ongoing drama on the nest. For these reasons, we have been quite guilty, at least until recently, of neglecting to study the behaviour of the wasps when they are away from their nests.

Once a year, we go through an elaborate ritual of interviewing and recruiting new students for our PhD programme at the Centre for Ecological Sciences, Indian Institute of Science. We finally welcome so few students from such a large pool of talented applicants that the process is somewhat of a lottery. Some years ago, my luck turned in this lottery when a young man named Souvik Mandal chose me as his mentor.

Souvik was very bright and had a kind of innate intelligence that could hardly be attributed to his formal education. But he was also anxious and restless, and having grown up in the small town of Berhampore, about 200 km north of Kolkata, he was struggling to find his bearings in the academic and social world of the big city. It soon became evident that sitting patiently in front of a nest for hours on end, as the junior-most member of the lab, was not Souvik's cup of tea – this bird had to be set free. I had long been interested in the 'outdoor' world of the wasps. When I suggested to Souvik that he explore the behaviour of the wasps away from their nest and the lab, he jumped at the idea.

Without a doubt, there is much to learn and admire the wasps during their sojourns away from their nests. How do the wasps find their way about? How do they manage to revisit a profitable source of food? How do they find their way back to the nest, especially after meandering to an unexpected location? Although wasps have been somewhat neglected in this regard, there is an enormous body of work on ants and bees, going back more than a hundred years. To begin your own work in such a richly studied area can sometimes be quite daunting.

When I was a student, we were mandated to study all the 'relevant' literature before designing our own research plans. I have always thought this was not a very smart thing to do. I fear that it is tailor-made to ensure that you work within the confines of an established paradigm and make, at best, some small incremental progress. But there seems to be great fear that, if you don't master the literature, you will do something that has already been done. Part of the reason for this paranoia is that we tend to bend over backwards to make our research far too complicated, structured and expensive than necessary.

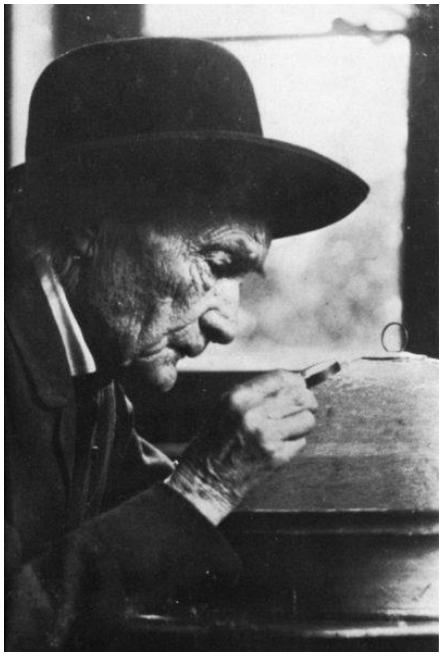
I think that we should go ahead and explore our common-sense ideas and learn by trial and error in a way that repeating what has already been done is not so costly. Indeed, it can help sometimes reconfirm past work and very likely show how past work can be improved or falsified. In this spirit, Souvik and I brainstormed about what he should do. I mentioned to him that I had often been frustrated by the fact that when I transplanted a nest to the laboratory, some wasps promptly returned to their original nesting site to build a new nest. Souvik told me that he had recently had the same experience.

So, our first set of questions were obvious. How far do the wasps fly in the course of their daily foraging duties so that they become familiar with the landscape, permitting them to return even if displaced involuntarily? Souvik thus decided to systematically displace wasps from their nests to different locations and see if they would return.

Displacing an animal from its location and observing its response is a very old trick. It was made famous by the French naturalist, entomologist and belletrist, Jean Henri Fabre (1823-1915). I love that he is called a 'belletrist', which my dictionary defines as "a person who writes essays, particularly on literary and artistic criticism, that are composed and read primarily for their aesthetic effect". I wish we did this more often. Reading Fabre's essays even in translation vindicates this title, but of course, his aesthetic effect has a sound scientific grounding. Little wonder that Fabre was dubbed "The Poet of Science" by his biographers and "The Homer of Entomology" by none other than Charles Darwin.

But even more impressive than his belletrism is Fabre's account of how he came to be a naturalist:

> "From my earliest childhood, I have felt drawn towards the things of Nature. It would be ridiculous to suppose that this gift, this love of observing plants and insects, was inherited from my ancestors, who were uneducated people of the soil and observed little but their own cows and sheep … Nor do I owe anything to a scientific training. Without masters, without guides, often without books, I have gone forward with one aim always before me: to add a few pages to the history of insects."



French naturalist Jean Henri Fabre. Photo: Félix Nadar (1820-1910), public domain

Fabre's description of his formal education reveals the truth behind his disdain for training: "In my early days, it was considered unwholesome for boys to be gay and active, so our system of education applied the remedy of melancholy and gloom. Our houses of instruction were above all houses of correction. In a yard between four walls, a sort of bear-pit, the boys fought to make room for their games under a spreading plane-tree. All round it were cells like horseboxes, without light or air: those were the class-rooms."

I saw clear echoes of many of these sentiments in Souvik and was convinced that he was ideally suited to play Jean Henri Fabre to our wasps. Fabre made many of his famous observations and experiments in a small piece of land "fenced in for the sake of privacy: a desolate, barren, sun-scorched bit of land, overgrown with thistles and much beloved by Wasps and Bees" which he obtained after forty years of struggle. The Indian Institute of Science campus, where Souvik did all his experiments, is far richer in biodiversity and came to him with no struggle, it must be noted.

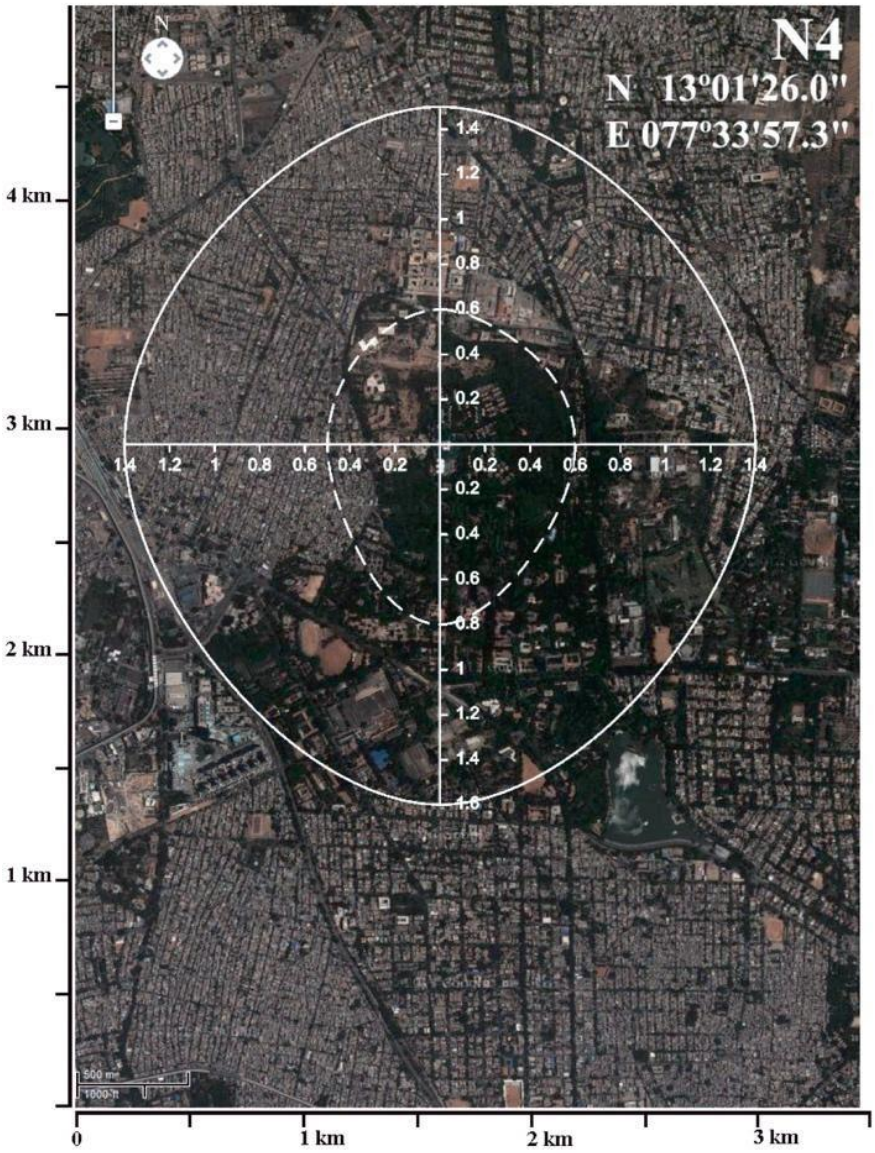
Souvik located four large, naturally occurring nests of *Ropalidia marginata* on the campus, painted all their wasps for individual identification and proceeded to observe them so as to identify the forager wasps who are expected to be familiar with the surrounding landscape. Then he visited each nest between 0600 and 0630 hrs before their first foraging trip of the day, removed all known foragers and placed them in aerated glass vials.

Between 0900 and 1030 hrs, he got on his bicycle and transported the vials containing the wasps in a polythene bag that neither blocked light completely nor permitted a view of the outside world. He then systematically released the wasps at 100 m intervals in four cardinal directions with respect to the nest. Having thus released the wasps, he bicycled back to the nest to await their return. In all, he released 249 forager wasps one or more times, amounting to a total of 486 releases.

Each night, he recorded the wasps present on each nest at 2100 to 2200 hrs to ascertain which wasps had made it back to the nest. If a wasp was not seen on the nest for three consecutive nights after its release, it was deemed lost. From some sites, all wasps successfully returned to their nests on the day of the release. Some or all wasps returned from other sites within three days but not on the day of release. From yet other sites, no wasp returned even after three days of release.

With this information, Souvik drew two imaginary boundaries around each nest. The first boundary enclosed all the points from which all wasps returned on the day of release. He called this the minimal homing area. The ability of a wasp to return home is called 'homing'. He calculated that the minimal homing area for *R. marginata* was 0.73 ± 0.25 km2 around the nest. The second boundary additionally enclosed the points from which at least some of the wasps returned within three days. He called this the maximal homing area, which was 6.22 ± 0.66 km2 around the nest.

We infer that the wasps routinely forage within the minimal homing area and therefore have no difficulty finding their way back to the nest. We also infer that some of the wasps could return from outside the minimal homing area but inside the maximal homing area, in spite of not being familiar with the landscape – these wasps may have used other means to find their nests, such as by conducting systematic searches.



A satellite image of the study site showing the position of one of the study nests. The inner broken line encompasses the minimal homing area and the solid outer solid line encompasses the maximal homing areas, of the wasps of this nest. Image: Souvik Mandal

It is not entirely clear why no wasps returned from outside the maximal homing area. Systematic searches from such a great distance may have been difficult, or they may simply have given up and built a new nest of their own. It may also be that if they returned after too long, they may have lost their nest identity (smell) or may lose their social status in the original colony.

We expect the minimal homing areas to depend on the distribution of food in the vicinity and the number of wasps and larvae that need to be fed. On the other hand, we expect the maximal homing

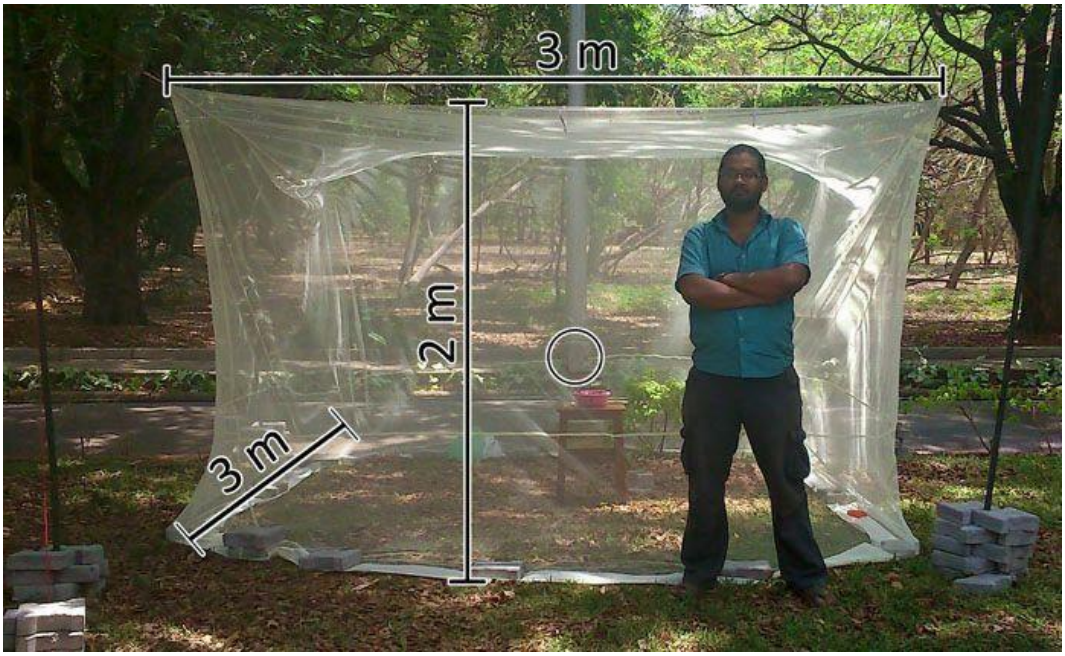
areas to be more independent of the particular nest or its location but be a characteristic of the species. Consistent with this reasoning, we found that minimal homing areas varied more from nest to nest than the maximal homing areas.

In collaboration with another of my PhD students, Anindita Brahma, Souvik went on to do many more interesting experiments, armed with little more than his bicycle, a compass and a video camera.

In one study, for example, Souvik and Anindita made some remarkable observations of the behaviour of the wasps they released. It is possible to record the initial orientation of the wasps by noting the compass direction in which the displaced wasp first disappears from view – this is tellingly called the "vanishing bearing".

Wasps released within their familiar area returned on the same day, but their vanishing bearings were surprisingly not in the homeward direction. This may be because, finding themselves in familiar territory, they were in no hurry to go home – why not gather some food before heading home. To test this conjecture, Souvik and Anindita offered food to the wasps just before releasing them. Now, these wasps oriented toward the nest and returned home sooner than the unfed wasps. However, when released outside the areas of their familiarity, some wasps oriented homeward and returned on the day of their release. Others oriented randomly and returned only after a day or two or not at all.

In another rather dramatic experiment, Souvik and Anindita managed to deny the wasps any familiarity with nearby places. They erected large mosquito net tents around the study nest, confining the wasps since birth, and provided them with food. Later such naïve wasps had more trouble returning home even from distances (outside the mosquito net) from which unconfined wasps return easily. If offered food, the naïve wasps oriented randomly, and only the older wasps returned after some delay. Even from a close but unfamiliar distance, the wasps presumably had to rely on other methods of finding their way home, and that ability seems to come with age.

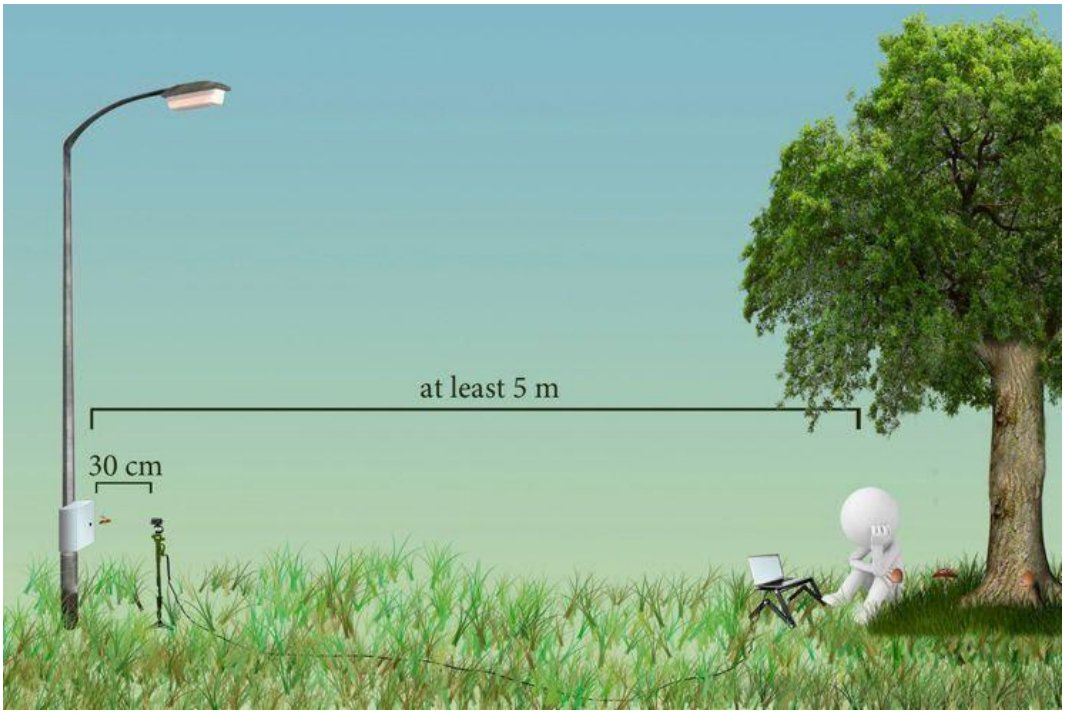


Souvik Mandal proudly posing in front of his mosquito net contraption, enclosing an experimental wasp nest. Photo: Souvik Mandal

Souvik likes to tell an interesting anecdote concerning the mosquito net experiment. One of his mosquito net-enclosed nests was rather conspicuously in front of the main administration building. He was promptly summoned by the Director of the Institute, but, to Souvik's great relief, rather than objecting to his activities, the Director was very curious about the experiment and listened to his story with great interest.

In another painstaking study, Souvik and Anindita recorded the exit, return and duration of absence, for wasps of different ages, on three nests for three consecutive days. From these data, they have

gained remarkably detailed knowledge about how the wasps learn their way around. As the wasps grew older and thus gained more experience, they developed preferences for flying off in specific directions, presumably reflecting their spatial memory of profitable sites. A particularly fascinating evidence of such learning was that while young and inexperienced wasps exited and returned in roughly the same direction, older and experienced wasps went one way and returned by another. Age and experience must make them sufficiently familiar with their surroundings to permit them to return home by novel routes.



A schematic representation of the set-up to record all outbound and return trips of all wasps. The experimental colonies were naturally found within electric boxes attached to roadside lampposts. A motion-sensitive video camera placed 30 cm away began recording automatically whenever a wasp came out or went inside the box. The timing of departure and arrival of every wasp as well as the foraged material could be retrieved from the video, stored in a laptop computer connected to the camera and placed at least 5 m away from the lamppost. Souvik, clad in camouflage attire, sat near the laptop and manually recorded the vanishing direction of the outbound and inbound foraging trips. Photo: Souvik Mandal

It is amazing how much one can learn by performing simple experiments driven by curiosity and imagination without fancy and expensive technology.

I do not want to leave the reader with the impression that Souvik permanently neglected the literature in this field. He used the clever strategy of reading some of the literature, doing some experiments, reading more, doing more, and so on, in a cyclic fashion. By the time he wrote his PhD thesis, he had gained such mastery over the literature that his introductory chapter reviewing the literature has since been published as an invited review article.

Putting his experience of chasing wasps on a bicycle to good use, Souvik Mandal now teaches a course on computational ethology at Harvard University. It has been my good fortune to have been his mentor.

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Gadagkar, R., 2021. More Fun Than Fun : Chasing Wasps on a Bicycle – and Getting a PhD. URL https://science.thewire.in/the-sciences/more-fun-than-fun-chasing-wasps-on-a-bicycle-and-getting-a-phd/