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Honey bee collecting nectar

War and Peace

Conflict and Cooperation in an Insect Society

UNKNOWN to many of us, a large number of insect species organize themselves into very sophisticated societies. Their societies parallel and sometimes surpass human societies in their social organization, in their social integration, in communication, in division of labour and most importantly in the way in which they tread a very fine balance between conflict and cooperation.

In a honey bee colony, for example, you may find fifty to sixty thousand individuals of which there is only one large fertile queen, a small number of males or drones, and the rest of the colony consists of small, sterile females who are referred to as workers. Together they function as a colony.

World of the Honey bee

The queen is typically surrounded by a small group of workers. It is the duty of these workers to take care of the queen. They lick, clean and feed the queen, who is so busy laying eggs and secreting pheromones that she has no time to take care of herself.

This job of taking care by the workers is done in shifts. A few minutes later these workers who are in-charge of the queen will go off elsewhere in the colony to perform other tasks, and other workers who have been performing other tasks will come to take care of the queen. This gives an opportunity for a very large fraction of the worker force to come into close contact with the queen and be aware of the state of their queen.

All the tasks that are required to run the society are actually done by the workers. The males – I am embarrassed to say – are incredibly lazy and they actually do not do any work for the honey bee society. It's the females who do all the work. In the first half of their lives workers work inside the colony – building the nest, cleaning it, feeding the larvae, processing food, guarding the nest, removing dead bees and so on. In the second half of their lives, they go outside the colony in search of food – nectar and pollen – for the colony.

Some of us may not be aware that honey bees have a fairly sophisticated symbolic language which is called the dance language. When a honey bee finds a large amount of food, she returns to the hive and is able to communicate with bees at home through this dance and provide information about the food she has found, how much, how far away from home, and exactly how to get there. And after she has performed this dance you can take the dancer away and those bees who have watched the dance will be able to go and find that particular source of food, which may well be five kilometers away from the hive. This is an accomplishment that no other animal species appears to have made other than human beings.

A typical nest of the primitively eusocial wasp *Ropalidia marginata* (Photo: Thresiamma Varghese)

Whether it is work distribution, choosing a leader or, for that matter, protecting colonies from foreign attacks, insect societies hold a mirror to us and make us think and reflect on the way we humans conduct our own affairs.

It is the dual ability to have peace with insiders and make war with foreigners that is perhaps the reason why the insect societies have been so ecologically successful as to have received the label "super organism".

The meek and docile queens of R. marginata became queens because they begin their career as extremely aggressive individuals. We labeled the hyper aggressive worker as the Potential Queen.

Wasp—At the Brink of Sociality

Wonderful as they are, I do not use honey bees in my research. The reason is that honey bees attained their sophisticated social organization many millions of years ago so that the details of their transition from solitary to social life has now become obscured. Instead, I use the primitively eusocial Indian tropical wasp *Ropalidia marginata.*

This is a remarkable wasp that appears to be at the brink of sociality. It can organize itself into reasonably sophisticated societies and yet it has not forgotten to lead a solitary life. Moreover, its societies (colonies) are small and often contain no more than 20-30 individuals. This allows us to mark every individual wasp with unique spots of coloured paint and study their behaviour.

My students and I have spent many years attempting to understand how and why these wasps organize themselves into social colonies. Our research has involved asking simple questions and designing experiments to answer these questions. Almost always a successful answer to a question opens up at least one new question that requires its own new experiment, provides a new answer, leads to yet another question and so on. Here I will give a small sample of such cycles of questions, experiments, answers and new questions.

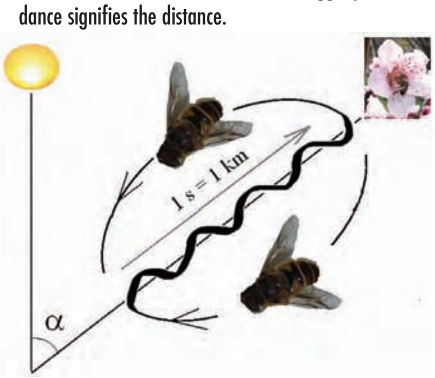
Incredible Behaviour

In an early study we asked how the individual members of a colony divide tasks among themselves. To answer this question we recorded the behaviour of all individually identified wasps and subjected the resulting data to multi-variate statistical analysis. The result was that we could identify three distinct groups of wasps that we labeled sitters, fighters and foragers.

This result led to the question about the position of the queen in the colony in such a system of behavioural caste differentiation. Queens of other such wasp species are known to be aggressive and use their physical aggression both to suppress worker reproduction and to regulate non-reproductive activities of the workers such as foraging and brood care. We therefore expected our queens to fall in the fighter caste. To our great surprise this was not the case. In colony after colony, we found that *Ropalidia marginata* queens belong to the sitter caste.

This result raises the question of how such meek and docile sitters are

The waggle dance - the direction the bee moves in relation to the hive indicates direction; if it moves vertically upwards the direction to the source is directly towards the Sun, the duration of the waggle part of the dance signifies the distance.



accepted as queens. To answer this question we designed an experiment that involved studying normal, queen-right colonies, experimental removal of the queens to study queenless colonies and reintroduction of the queen to study the reconstituted colony.

Such experiments yielded the remarkable result that the normally peaceful society of *Ropalidia marginata* became extremely aggressive upon removal of the queen. Even more remarkably, the new aggression was entirely shown by a single worker. Equally remarkably we found that this hyper aggressive individual dropped her aggression and went back to work immediately upon return of the queen. We also found that if the queen was not returned, the hyper aggressive individual gradually lost her aggression in about a week's time and became the next meek and docile queen of the colony.

So, the meek and docile queens of *R. marginata* became queens because they begin their career as extremely aggressive individuals. We labeled the

Bees Signal Danger

A biologist at UC San Diego has discovered that honey bees warn their nest mates about dangers they encounter while feeding with a special signal that's akin to a "stop" sign for bees.

The discovery, detailed in a paper in the February 23 issue of the journal *Current Biology*, resulted from a series of experiments on honey bees foraging for food that were attacked by competitors from nearby colonies fighting for food at an experimental feeder. The bees that were attacked then produced a specific signal to stop nest mates who were recruiting others for this dangerous location. Honey bees use a waggle dance to communicate the location of food and other resources. Attacked bees directed "stop" signals at nest mates waggle dancing for the dangerous location.

James Nieh, an associate professor of biology at UCSD who conducted the experiments, said this peculiar signal in bee communication was known previously by scientists to reduce waggle dancing and recruitment to food, but until now no one had firmly established a "clear natural trigger" for that behavior.

The stop sign is a brief vibrating signal made by the bee that lasts for about a tenth of a second with the bee vibrating at about 380 times a second. "It is frequently delivered by a sender butting her head into a recipient, although the sender may also climb on top of the receiver," Nieh said. Bee researchers originally called it a "begging call," because they believed the signaling bee made it to obtain a food sample from the receiver.

But Nieh discovered in his experiments that one trigger for this signal – which caused the waggle dancers to stop and leave the nest – was attacks from bee competitors and simulated predators. The more dangerous the predator or competitor, he found, the more the stop signals bees produced to stop other bees from recruiting to that location. Thus, fewer nest mates go to the dangerous food site.

Nieh found in his experiments that during aggressive food competition, attack victims significantly increased their production of stop signals to nest mates, some by more than 40 times. Bees foraging for food that attacked other bees or experienced no aggression did not produce stop signals. But bees exposed to a "bee alarm pheromone" increased their stop signaling by an average of 14 times. Those whose legs were mechanically pinched in a simulated bite increased their stop signals by an average of 88 times.

(Courtesy: www.sciencedaily.com)

Road to Royalty Begins Early

Social status in paper wasps is established earlier in life than scientists thought, says a recent study published in the journal *PLoS ONE*.

While many social insects have distinct social classes that differ in appearance and are fixed from birth, paper wasp society is more fluid – all castes look alike, and any female can climb the social ladder and become a queen. Now, molecular analysis reveals that paper wasp social hierarchy is less flexible than it appears. Queens diverge from their lower-status sisters long before they reach adulthood, scientists say.

Slender reddish-brown wasps with black wings, *Polistes metricus* paper wasps are a common sight throughout the Midwestern and Southeastern U.S. Female wasps develop into one of two castes that take on different roles within the nest. While young queens don't work and eventually leave the nest to reproduce and rule colonies of their own, workers forego reproduction and spend their lives defending the nest and raising their siblings.

"All offspring look alike but some work and some don't," said lead author James Hunt. "The workers are the ones that fly out and sting you if they feel their colony is threatened."

Hunt and his colleagues wanted to find out if hidden molecular mechanisms set some paper wasps on the path to becoming workers, and others to becoming queens. "Many scientists think that paper wasp social status isn't decided until they are adults, but some think there is more to it than that," said Hunt.

With co-authors Amy Toth and Tom Newman at the University of Illinois and Gro Amdam and Florian Wolschin at Arizona State University, the researchers measured gene activity and protein levels in young paper wasp larvae before they took on different roles.

Although all wasp larvae look and act alike, the researchers discovered several differences during development that predispose them to one caste or the other. The larvae that become queens have high levels of a group of proteins that enable them to survive the winter and reproduce next year, whereas the ones that become workers are much shorter-lived and have low levels of these proteins.

Future queens also showed higher activity of several genes involved in caste determination in other, more recently evolved insects that have more visible distinctions between castes. "Paper wasps and honey bees are separated by 100 million years of evolution, but we see some of the same gene and protein patterns in paper wasps that lead to different types of adults in bees," he explained.

The results help shed light on how insect social behavior comes to be, Hunt explained. "It is sometimes argued that adult wasps actually choose to become workers in order to help their mother reproduce and raise their sisters — hence the term 'altruistic,'" he said. "What we found is that really the choice is limited by how they develop as larvae."

(Courtesy: www.sciencedaily.com)

hyper aggressive worker as the Potential Queen (PQ).

But this raises another question: How do they suppress worker reproduction and maintain reproductive monopoly throughout their tenure (which may last several months) after losing their aggression within a week. To answer this question we designed a different experiment.

Here we cut a nest into two parts and separated them by a wire mesh partition and released the queen and half the workers on one side and the remaining workers on the other side. Our expectation was that the queen might be using a pheromone to signal her presence to the workers. Our prediction was that if the pheromone is volatile, it will be perceived across the wire mesh so that workers on both sides of the mesh will behave as if they have a queen. On the other hand, if the pheromone is non-volatile, workers in the queenless side will behave as if they do not have a queen; in other words one of the workers on this side should become hyper aggressive and behave like a PQ. We have repeated this experiment several times and in every case the queenless side produced a PQ indicating that the queen pheromone is non-volatile.

Lazy males made to work (Photo: Sujata Kardile)

The non-volatile queen pheromone may be adequate to suppress worker reproduction but how does the meek and docile queen make its workers work for the colony? This question needed yet another experiment. In this case we found by removing the queen and observing the workers that the queen does not regulate the work of the workers. The workers themselves regulate each other's work in a decentralized, self-organized manner, irrespective of whether the queen is present or not.

But how is the PQ chosen among all the workers. We have performed many different kinds of experiments in our attempts to answer this question but so far we have failed. The PQ is an unspecialized individual, not different from other workers in her morphology, body size, behaviour, dominance rank or her ovarian development. Although we cannot predict the identity of the PQ in the presence of the queen, we asked if there was nevertheless a designated heir known and acceptable to the rest of the colony. Performing other more complicated experiments, we have found clear evidence that there is indeed a cryptic

The queen bee with workers at its service (eft) and a worker bee (above)

In a honey bee colony, for example, you may find fifty to sixty thousand individuals of which there is only one large fertile queen, a small number of males or drones, and the rest of the colony consists of small, sterile females who are referred to as workers.

heir designate known and acceptable to the wasps although unknown to us.

A striking feature of the wasps evident in all these experiments is that they managed their affairs including the contentious task of designating a PQ without over conflict. Conflict however was very conspicuous in the manner in which the wasps behaved towards members of other colonies.

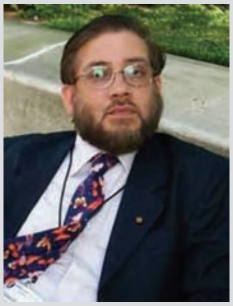
Using another set of experiments we showed that the wasps have a well-developed mechanism of nest-mate discrimination. This ensures that alien wasps are kept away from nests when we experimentally introduced foreign wasps into the cages of other colonies; the resident wasp displayed a very nuanced reaction to the introduced foreigners.

The young members of the foreign colony were allowed to join the resident colony. The older workers of the foreign colony were allowed to live in the periphery of the cage but not allowed to join the colony. The queen of the foreign colony was located wherever she was and killed!

In subsequent experiments, we have shown that the young foreign wasps allowed to join the colony became fully integrated into their foster colonies and lose their foreign identity. Indeed they can go on to become foragers and even future queens of their foster colonies.

In summary, we find that the wasps have well-developed mechanisms to maintain peace within the colony and equally well-developed mechanisms to make war with foreigners. It is this dual ability to have peace with insiders and make war with foreigners that is perhaps the reason why the insect societies have been so ecologically successful as to have received the label "super organism".

One might say, we humans are not very different. I certainly do not think that we should blindly imitate insect societies. But I do think that insect societies hold a mirror to us and make us think and reflect on the way we humans conduct our own affairs. ■



This article is based on a lecture delivered by Prof. Raghavendra Gadagkar at the "CSIR Foundation Day Lecture" at Vigyan Bhavan, New Delhi on 26 September 2010.

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