How to Design Experiments in Animal Behaviour*

6. Why are Male Wasps Lazy?

Raghavendra Gadagkar

In this article, we move from sensory physiology to psychology and consider the proverbially lazy drone. I will describe how some simple experiments permitted us to understand why males in the Indian paper wasp *Ropalidia marginata* do no work in the colony even during the time they live in it. Taking the behaviour of feeding larvae as an example of work, we show that male wasps normally do not feed larvae, not because they are incapable of doing so, but because they do not have access to enough food and also because female wasps are so much better at this job. As a confirmation of this conclusion, we could cure the males of their laziness, i.e., get them to feed the larvae by providing them with excess food and leaving them in the presence of hungry larvae, without the presence of females.

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From Sensory Physiology to Psychology

In the first five articles in this series, we focussed on how animals perceive their environment using their senses of vision and smell, and modulate their behaviour appropriately to solve complex problems necessary for their survival. We used their behaviours as reporters of their sensory capabilities. We saw how simple experiments permitted us to conclude that digger wasps use vision to learn the features of the landscape around their nests, that honey bees have well-developed colour vision, that ants use pheromone trails to choose the shortest path to their feeding sites, that honey bees use optic flow to estimate distance flown and that some ants count their steps to estimate the distance they have

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walked. Of course, sensory inputs were processed in the brains of the insects before they produced the appropriate behaviour. Nevertheless, there was a relatively more direct connection between the sensory input and the motor output. From such sensory physiology, we will now consider phenomena more in the realm of psychology, where the cause-effect relationship between sensory input and motor output will be more indirect, delayed and complex. In this article, we will consider the 'laziness' of male wasps and see how similarly simple experiments can help us conclude that male wasps are lazy, understand why they are lazy and, incredible as it may sound, cure them of their laziness.

The Saga of the Honey Bee Queen

Without realizing that the honey bee colony's 'leader' is a female bee, one John Knox published a treatise in 1558 entitled *First Blast of the Trumpet Against the Monstrous Regiment of Women* in which he argued against the rule of women such as Queen Elizabeth, on the grounds that "Nature hath in all beasts printed a certain mark of dominion in the male, and a certain subjugation in the female."

Every high-school student today knows that honey bees live in populous colonies consisting of a single large queen bee, a few lazy drones and thousands of worker bees that can give you a mildly painful sting if you mess with them. But our understanding of the honey bee queen has a surprising history. Honey bees have been known to humans and have sweetened their lot with their honey, since long before recorded history. However, our wise men (females having been forcibly excluded from the intellectual affairs of society), could neither imagine nor accept that the honey bee colony could be 'headed' by a female bee! Aristotle pronounced that honey bee colonies are led by a King. Without realizing that the honey bee colony's 'leader' is a female bee, one John Knox published a treatise in 1558 entitled *First Blast of the Trumpet Against the Monstrous Regiment of Women* in which he argued against the rule of women such as Queen Elizabeth, on the grounds that "Nature hath in all beasts printed a certain mark of dominion in the male, and a certain subjugation in the female." The cleric Charles Butler, however, seems to have made amends in 1609 by referring to the honey bee colony as a 'feminine monarchy' but he must have only guessed rather than actually known the correct sex of the "leader". It was only in the seventeenth century that the Dutch anatomist Jan Swammerdam demonstrated that the 'King' bee contained ovaries with eggs [1, 2]. If this was not irony enough, it turned out that the male bees, rather than have 'a certain mark of dominion', are lazy, i.e, they do not participate in colony labour, and are at the mercy of the female bees for their food, until they leave the nest of their birth and die in the act of mating or be dragged by their legs and ejected from the colony by their sisters (for overstaying!). But why are the males so lazy?

One Question, Two Answers

Why indeed are the males lazy? When a biologist asks 'why', there are two distinct kinds of answers possible and both are appropriate, and neither is more nor less valid than the other. Consider, for example, the following 'why' question in the context of a very different kind of animal and a very different kind of phenomenon. Every year Siberian cranes migrate 6400 kilometres from their breeding grounds in Siberia and arrive in the Bharatpur bird sanctuary in Rajasthan in North-Western India. Now why should they do something so risky and audacious? One kind of answer to this 'why' question has been painstakingly put together with much research over many years using a variety of different migratory birds. The birds migrate because, at the onset of winter, the shortening day lengths in the northern latitude are sensed by their pineal gland which in turn leads to hormonal changes in the birds, ultimately leading to what is tellingly called 'migratory restlessness' and produces the urge to migrate. The migratory routes appear to be genetically fixed, as research on another bird, the blackcap, has shown. This is a perfectly legitimate answer to the 'why' question and is championed by physiologists and others who revel in unravelling the mechanistic causes of behaviour. Such answers are labelled as 'proximate' answers or mechanisms. On the other hand, more evolutionary minded biologists seek to understand why natural selection has favoured such unusual behaviour over simply staying back in Siberia during the harsh winters. They focus on the possible advantages of better survival and feeding in the relatively warmer climate in Bharatpur, and attempt to evaluate whether these advantages offset the disadvantages of

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the costly and risky journeys involved. Such answers are equally (but no more) legitimate and are labelled as ‘ultimate’ or ‘evolutionary’ answers or mechanisms [3].

Some researchers have attempted to provide an ultimate answer to the question of why the ant, bee and wasp males are lazy. In other words, they argue that the altruistic sterile worker strategy is likely to yield more evolutionary fitness for females than it does for males. Relatively speaking, males get more fitness by going off to reproduce on their own by mating with females from other nests.

Similarly, some researchers have attempted to provide an ultimate answer to the question of why the ant, bee and wasp males are lazy. In other words, they argue that the altruistic sterile worker strategy is likely to yield more evolutionary fitness for females than it does for males. Relatively speaking, males get more fitness by going off to reproduce on their own by mating with females from other nests. This has to do with the peculiar haplodiploid genetics of the Hymenoptera where males are haploid, and females are diploid. But I will not go into that here both because it is a somewhat complicated theoretical argument and also because it cannot be verified by simple experiments. Instead I will focus on possible proximate answers to the question of male laziness. And, to do so, I will take you to the wonderful world of the Indian paper wasp *Ropalidia marginata*.

The Primitively Eusocial Wasp *Ropalidia marginata*

I joined the Central College in Bangalore to pursue BSc (Hons) and MSc in zoology in 1969. The first thing I saw was that every window of the zoology and botany department buildings had one or more nests of the social wasp *Ropalidia marginata* (*Figure* 1). I was surprised that my zoology teachers could tell me nothing about these insects – they were only knowledgeable about the exotic species described in our textbooks, which were mostly written (or copied from) textbooks written in the UK or USA. These living, local insects fascinated me much more than those that resided in my textbooks, and I have never stopped watching and studying them till today. *R. marginata* is a primitively eusocial wasp that is widely distributed in peninsular India. They are called paper wasps because they build their honeycomb-like nests from paper, which they manufacture by scraping cellulose fibres from plants, adding some salivary secretions and making a fine pulp. I will have the opportunity to give several interest-

Figure 1. A typical nest of the Indian paper wasp *Ropalidia marginata*, showing several adults and cells with brood in various stages of development. (Photo: Dr Thresiamma Varghese).

ing facts about this species in the next few articles in this series. For the purpose of this article, all we need to know is that their colonies comprise several females, only one of which lays eggs and is called the 'Queen'. The remaining female wasps function as sterile workers, cleaning and guarding the nest and making trips away from the nest to bring back small insects and spiders to feed the larvae, and cellulose fibres to build the nest. There may also be a few males about which we will see more below, but make no mistake, *R. marginata* is as much a feminine monarchy as Charles Butler's honey bee colonies [4].

Are Males of *R. marginata* Lazy?

When we study these wasps, we mark all individual wasps with one or more spots of non-toxic, odourless and quick-drying paints of different colours on different parts of their bodies to individually identify every wasp. We mark the wasps without capturing them, but by patiently waiting for them to be busy doing something when we opportunistically apply small spots of paint on them with a fine toothpick or broomstick. We have developed a

Figure 2. The brown faces of *R. marginata* females (top) and yellow faces of the males (bottom). The mandibular plate that shows the clearest colour variations between the sexes is called the clypeus. (Photo: Dr Thresiamma Varghese).

system to thus uniquely mark and name thousands of wasps that would otherwise look alike.

This allows us to follow the behaviour of individually identified wasps for many days, and even over their entire lifespan. During the marking process, we encounter the occasional male wasp. We can easily distinguish males from female wasps because of their yellow faces as compared to the browner faces of the females (*Figure* 2). If you watch a nest containing marked male and female wasps, your first impression would be that the female wasps are usually very busy working or fighting, but the males are doing nothing. But such first impressions are not good enough to conclude that male wasps are lazy. If we follow the fates of male and female wasps since their eclosion from their pupal cases, we find that female wasps remain on their nests of birth for 27 ± 23 (range = 1–106) days. However, the male wasps stay on their nests of birth only for 6 ± 2.6 (range = 1–12) days, during which they never leave the nests and after which they leave permanently, never to return and never to visit any other nests. They spend the rest of their lifespan leading a nomadic life and mating with females that may be out foraging. This behaviour of mating away from the nest must have evolved to avoid inbreeding. So, if males are hardly present on the nest, how can we accuse them of laziness. Thus, we must specifically focus on males at the time they

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are still present on their nests, i.e, before they leave. But these males may not work because they are too young to work. The appropriate test then is to compare the rates of work performed by males while still living on the nest with the corresponding rates of work performed by the similarly aged female wasps.

I had the good fortune of being joined by a student passionate about understanding why males are lazy, although we certainly had no idea at that time that we might actually be able to cure them of their laziness. It is perhaps not so surprising that the student passionate about this topic was a female student. Indeed, Ruchira Sen (*Figure* 3), who joined my laboratory to do her PhD in 2002, took the unusual step of devoting her entire PhD work to males of *R. marginata*. This was quite unusual for any research group studying social Hymenoptera and was a first for my group. Not surprisingly, female ants, bees and wasps have been the focus of most attention – after all, they are the stuff of feminine monarchies! But I think Ruchira chose to study males because she was bold enough to take the path less trodden, but I also suspect that male laziness did not appeal to her female sensibilities. Either way, I lucked out by having a student passionate about her research – passion is what drives most successful scientists and sustains them through back-breaking work that most friends and family do not appreciate or understand. Ruchira and I decided to focus on the behaviour of feeding larvae as the example of work. Feeding larvae is one of the most conspicuous and important tasks that adult wasps perform on the nest because the larvae are completely helpless and at the mercy of adults who have to insert food into their mouths several times a day.

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Ruchira promptly set about comparing one-week-old female wasps with one-week-old male wasps in the rates at which they both fed larvae. This is not as simple as it sounds. The behaviour of feeding larvae is easy enough to identify – it involves the adult wasps with solid food in their mandibles inserting their heads into larval cells and rapidly vibrating their wings; the absence of wing vibration suggest that they changed their minds and did not feed that larva. The real problem is to get unbiased estimates of feed-

Figure 3. Ruchira Sen (left) with the author (right).

ing rates by males and females. In studies of animal and human behaviour, it is much easier than you might think, to (subconsciously) bias your observations to find the pattern you expect to see or that you approve of. Observing animal behaviour may sound easy, but converting the observations into reliable quantitative data is fraught with difficulties. Recall the description of ethology by the Medawars, quoted in the first article in this series [5] "*Ethology is rooted in observation of animal behaviour, an activity that only simpletons think simple.....Observation is a difficult and sophisticated process...*". At the very beginning of my research career, when I decided to devote myself to the study of the behaviour of *R. marginata*, I standardised a set of sampling methods designed to provide as unbiased estimates of behaviour as possible. These include instantaneous scans, recording all occurrences of rare behaviours, focal animal sampling and focal behaviour sampling. An important trick to reduce subconscious bias is to reduce the number of individual or behavioural events that have to be recorded, per unit time. If we try to record more than is easily possible, then our mind will pick what it likes. The instantaneous scans (scans, for short) which involve scanning the nest and recording only the very first behaviour we see each wasp performing leaves little room for bias. In recording all occurrences of rare behaviour ('all occurrences', for short), again there is less chance of subconscious bias because rare behaviours are just that

– rare. In the focal animal and focal behaviour sampling, we randomly pick just one animal or just one behaviour to observe at any given time, once again, reducing the opportunity for our minds to pick [4]. Using these methods, Ruchira proceeded to measure and compare the rates at which 1–6-day-old male wasps and 1–6-day-old female wasps fed the larvae. As we had expected from previous more casual observations, males hardly ever fed the larvae, while the females fed the larvae at significantly higher rates. This striking difference between male and female behaviour was made even more striking by the fact that the males fed themselves at about the same rates as the females did (*Figure* 4). So, male *R. marginata* are lazy indeed [6].

Three Hypotheses for Male Laziness

Having confirmed that the male wasps are indeed lazy, we proposed three testable hypotheses that can potentially explain why they are lazy. Let me reiterate that these hypotheses are meant to provide proximate (and not ultimate) explanations, as discussed above.

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Hypothesis A

Males are simply incapable of feeding larvae. Feeding the larvae with solid food may require a certain amount of skill, involving judging larval hunger levels, the size of the food bolus that needs to be offered, the appropriate duration of feeding, etc. It is, therefore, not unreasonable to imagine males do not have these skills, especially because males in solitary wasps also do not feed larvae.

Hypothesis B

Males never get access to enough food to satisfy themselves and have something leftover to offer to the larvae. This is quite plausible because males do not forage while on the nest in this species, as in all social Hymenoptera, and thus have to depend on the females for their supply of food. In some species, such as honey

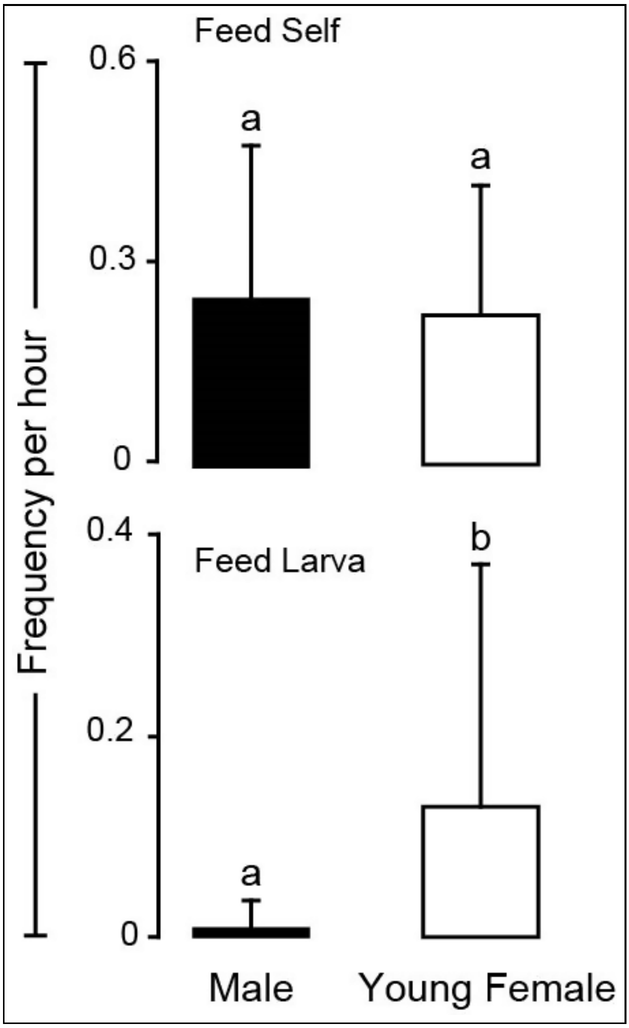

Figure 4. A comparison of male wasps (who stay on the nest for only about 6 days after eclosion) and 1–6-day female wasps of *R. marginata*. While male and female wasps feed themselves at comparable rates (top), males almost never feed larvae but females feed larvae at a significantly higher rate (bottom). Bars with different letters are significantly different from each other ($P < 0.007$, Mann–Whitney U test). (Redrawn with permission from [6]).

bees, females are known to withhold food from males in times of shortage. Besides, males are not aggressive enough to be able to forcefully snatch food from females.

Hypothesis C

Females are so much more efficient at feeding the larvae that they leave no opportunities for the relatively inefficient males to do so. This may sound cheeky, but it is easy to imagine that larvae prefer to be fed by the more efficient females. More importantly, it is an eminently testable hypothesis, as you will see below.

Testing the Hypotheses

We set up the following experimental design to test these three hypotheses. We collected 14 naturally occurring nests of *R. marginata* from in and around Bangalore and transplanted them along with the brood and all adult wasps into our Vespiary. Early in my research career, I was able to design and construct a simple but very special laboratory for housing and studying the wasps which I call the Vespiary. This laboratory is nothing but a room measuring approximately 10 m $\times$ 6 m $\times$ 5 m and is covered on all four sides by a wire mesh with openings 0.75 cm $\times$ 0.75 cm (*Figure* 5). The mesh size is such that it allows *R. marginata* to fly in and out but keeps out its slightly larger predators namely the hornets *Vespa tropica* and *Vespa affinis*. Inside the Vespiary, we can keep the wasps in small plastic boxes, wood and wire mesh cages of various sizes and simply transplant them in the open, so that wasps can fly in and out. In the open transplants, the wasps forage on their own and are free to leave and build their nests elsewhere. Other wasps are also free to fly in and build their nests inside. Other than the useful convenience that they are protected from their main predators, these are essentially natural colonies. Much of our research is carried out in the Vespiary. The 14 nests brought in for this study were transplanted in the open so that the colonies were free foraging. As is our usual practice, all wasps in all the colonies were marked for unique identification.

The 14 nests were arbitrarily assigned to one of four types of experimental treatments.

In Type 1, we did nothing more, i.e., the wasps had to find food on their own and do as they please. We worried that the rates at which these wasps might find and bring food back to their nest and feed their larvae would be subject to the vagaries of the environment. If we were unlucky, we might not record enough instances of larval feeding behaviour, even by the female wasps, let alone by the male wasps, to be able to get statistically meaningful

Figure 5. A view from inside the Vespiary showing little plastic boxes and small and large cages used to rear wasps. Notice that the whole room is enclosed with a wire mesh screen instead of walls. For the experiments described here (and for most experiments) we leave the doors of the cages open so that the wasps are at liberty to come and go as they like and have to forage for themselves. (Photo: Dr Thresiamma Varghese).

data.

Therefore, in Type 2 nests, we provided them with a food supplement. This comprised 10 *Corcyra cephalonica* larvae, honey, and water placed in a petri dish 3 cm away from the nest every day. *C. cephalonica* is the common pest moth that infests stored rice and is easy to culture in the laboratory. We feed the moth larvae to the wasps kept in closed cages, where they thrive and reproduce well on this diet. Such a predictable supply of food close by, we hoped, would give us more opportunities to witness larval feeding behaviour.

In Type 3 nests, we removed all the female wasps and left the larvae with only the male wasps. This we hoped would encourage the male wasps to feed the larvae, if they could. The problem, of course, was that male wasps do not forage on their own and depend on the females to bring them food. To overcome this problem, we decided to hand-feed the male wasps ourselves. At first, we were not sure if this is possible. But Ruchira, with her patience and skill, succeeded admirably. She would take small pieces of *C. cephalonica* larvae with a long thin stick and hold them close to the male's mouth. At first, the males were afraid to approach but when they sensed that food was available without any harm, they readily accepted the food. She thus fed them to satiation, i.e, until they accepted no more. We hoped that this procedure would leave them with enough food and more so that they might feed the excess food to the larvae if they could do so.

Type 4 nests had a very different purpose. If males could indeed feed larvae and did so in Type 2 or at least in Type 3 nests, we wanted to study male feeding behaviour in detail and compare it with female feeding behaviour. After all, we would witness, if we were lucky, a very rare behaviour and the opportunity to describe it in detail was not to be missed. One of our hypotheses was that males are incapable of feeding larvae. In the event of having to reject this hypothesis, we had to be fully ready to capitalize on the opportunity that males could feed larvae. Given that males rarely feed larvae, their method of feeding, when they did so under special circumstances, needed to be compared with the corresponding behaviour of females who feed larvae as a matter of routine. The chances of males feeding larvae in Type 2 nests were small, but we had pinned our hopes on their doing so in Type 3 nests. In order to potentially compare the method used by males to feed larvae in Type 3 nests, where they were hand fed, we similarly hand-fed female wasps with pieces of *C. cephalonica* larvae in Type 4 nests.

To estimate the rates at which male and female wasps performed various behaviours, including feeding self, feeding larvae, masticating food, etc., Ruchira used scans and 'all occurrences' methods. But to provide a detailed description of the behaviour of feeding larvae by males and females in Type 3 and Type 4 nests respectively, she used the focal behaviour sampling, focussing only on feeding larvae and associated behaviours. Here, she began her observation when an adult wasp, male or female as the case may be, obtained food and continued focussing on that individual until all its food disappeared. Thus, Ruchira could obtain 325 h of observational data from the 14 nests put together.

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Males Can Feed Larvae and They Do Even Better in The Absence of Females

In Type 1 nests, males, as expected, did not feed the larvae, but females did so at a small rate. In Type 2 nests, with a food sup-

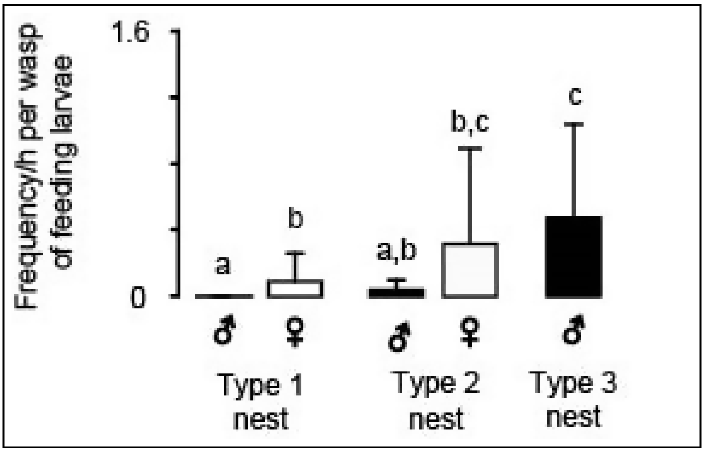

Figure 6. Mean and standard deviation of the rates at which male and female wasps feed larvae in Type 1 nests (no food supplement), Type 2 nests (with food supplement) and Type 3 nests (males were hand-fed and females removed). Bars with different letters are significantly different from each other (Mann–Whitney U test, with Bonnferroni correction, $p < 0.05$). [Redrawn from [7]).

plement, both males and females increased their rates of feeding larvae although the male rate was not statistically significantly different from zero. In Type 3 nests where there were no females, and the males were hand-fed and exposed to hungry larvae, male wasps fed larvae at a significantly higher rate, which is not statistically significantly different from the female feeding rates in Type 2 nests (*Figure* 6). We were convinced that the males were not simply getting rid of the food that they did not want but were actually seeking out the most appropriate larvae to be fed. For one thing, males did not simply dump unwanted food on the floor but delivered it to the cells in the nest. Second, they never delivered food to empty cells, egg cells or even to cells with very small larvae. Ruchira observed the males feeding larvae 345 times, and in 340 of these, they fed the largest class of larvae. Finally, in order to feed the larvae, males (in Type 3 nests), like the females (in Type 4 nests), performed a complex series of behaviours – they moved about the nest with a piece of solid food in their mandibles, checking out various cells and their contents with their antennae, apparently searching for cells bearing large larvae, and having found one, they inserted their head and thorax into the chosen cell, holding on to the food at one end, in a way that made it possible for the larvae to grab the food at the other end, and only then did they let go of the food.

Clearly, hypothesis A, that males are incapable of feeding larvae, can be rejected. Since males began to feed larvae in Type 2 nests while they did not do so at all in Type 1 nests, hypothesis B, that males rarely feed larvae because they rarely have access to enough food, is upheld. Because males fed larvae at higher rates in Type 3 nests (in the absence of females) compared to their own rates in Type 2 nests (in the presence of females), hypothesis C that males do not feed larvae because females do a much better job, is also upheld. Well, at least males did not feed larvae much when females were present and were feeding the larvae. Although this is not explicit proof that females do a much better job, it suggests that females, for one reason or another, inhibited the males from feeding the larvae. But do the males really do a bad job?

A Twist in the Tale

It was heartening to know that males are not incapable of feeding larvae and that they indeed fed larvae when they have enough food and especially when the females are absent.

It was heartening to know that males are not incapable of feeding larvae and that they indeed fed larvae when they have enough food and especially when the females are absent. Not only did we discover the reason for male laziness, but we could cure them of their laziness, by providing them excess food and leaving them in the presence of hungry larvae and with no females. We were delighted to publish a paper with the title 'Males of the social wasp *Ropalidia marginata* can feed larvae, given an opportunity' [7]. But alas, there was a twist in the tale, or a sting in the tail, as Roald Dahl would have put it. Many of the larvae in the exclusive care of the males, died. Now, why should this be so? We obtained some additional fascinating insights by making a detailed comparison of the behaviours of males and females feeding larvae in Type 3 and Type 4 nests, respectively. Upon acquiring solid food, adult wasps move from one larval cell to another, feeding bits of it to different larvae, all the while masticating it and imbibing some of the juices themselves. We defined a feeding bout as the time between an adult wasp acquiring a bolus of food and the food completely disappearing from its mandibles. Such a bout may have several episodes of feeding larvae interspersed with episodes of masticating, the latter representing self-feeding. We calculated the total duration of such feeding bouts for males and

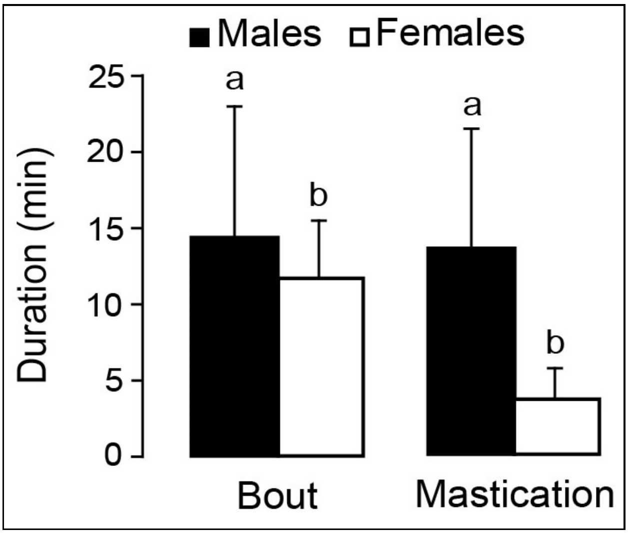

Figure 7. Mean and standard deviation of the durations of feeding bouts and mastication by male and female wasps. Statistical comparisons are by t test, separately for bout duration and mastication. Bars carrying different letters are significantly different ($P < 0.05$).

females as well as the duration of mastication within the feeding bouts. Males had significantly longer feeding bouts than females but more interestingly, males spent significantly more time masticating the food than did females. While females spent about a third of the feeding bout in masticating and the remaining time feeding the larvae, males spent over 90% of the bout masticating and less than 10% of the time feeding the larvae. Males thus masticated more and fed larvae less (*Figure* 7). Since adults imbibe juices in the food for themselves during mastication, we suspect that males drink most of the juices and feed much less nutritive fibre to the larvae. This may be why the larvae in their care died. But of course, males may have weaker mandibles and may require more time to masticate. At present, we do not have direct proof that males feed nutritionally impoverished food to the larvae, but this can be tested. Ruchira has found ways to snatch the bolus of food, from both males and females, just before they were about to offer them to the larvae. I am in search of a student to perform a comparative nutritional analysis of what males and females offer to the larvae and test this hypothesis. Until then, I better not pronounce the males 'guilty'!

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Reflections

In reflecting on the experiments described in this article, my student Ruchira's passion for research, her confidence and courage in walking the less-trodden path during her PhD, her skill and patience in hand-feeding the wasps, and her female sensibilities in tackling the question of male laziness, all come to mind. In addition, I wish to reflect on two additional features of scientific research that these experiments draw our attention to – the source of hypotheses, and funding for research.

The Source of Scientific Hypotheses

In science, the source of a hypothesis is not important as long it is testable and potentially falsifiable. I have already mentioned that our hypothesis C, namely that male wasps may not feed larvae because females are so much better at it, may seem a bit far-fetched but the source of the hypothesis is irrelevant as long as they are testable. Let us dwell on this a bit more. The misleading way in which we write our scientific papers is responsible for the erroneous impression among many scientists and especially among the public that all scientific hypotheses are generated by a logical, scientific process. In a thought-provoking essay, Peter Medawar (1961) asked "Is the scientific paper a fraud?" and answered in the affirmative. Since this is a serious charge, let me quote him verbatim.

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"*As to what I mean by asking 'is the scientific paper a fraud?' – I do not of course mean 'does the scientific paper misrepresent facts', and I do not mean that the interpretations you find in a scientific paper are wrong or deliberately mistaken. I mean the scientific paper may be a fraud because it misrepresents the processes of thought that accompanied or gave rise to the work that is described in the paper. That is the question, and I will say right away that my answer to it is 'yes'. The scientific paper in its orthodox form does embody a totally mistaken conception, even a travesty, of the nature of scientific thought...Hypotheses arise by guesswork. That is to put it in its crudest form. I should say* *rather that they arise by inspiration; but in any event they arise by processes that form part of the subject-matter of psychology and certainly not of logic, for there is no logically rigorous method for devising hypotheses.*"

This is a very short excerpt – the full essay is well worth reading. In short, hypotheses can come from anywhere, even from your dreams, but they must be capable of being put to the test, and it must be possible to disprove them, at least in principle. We must only label an idea as a scientific hypothesis if there is a way to show that it is wrong.

Funding for Science

As it should be obvious, the research described in this article, required no money or any sophisticated laboratory facilities.

As it should be obvious, the research described in this article, required no money or any sophisticated laboratory facilities. Anybody could have performed these experiments. And yet these experiments have shown for the very first time that a proverbially lazy hymenopteran male can work, given an opportunity. They also show why, at least in one species, the males rarely work, and this paved the way to experimentally cure them of their laziness. The fact that they could be cured of their laziness is further proof of our conclusion about why they rarely work. The twist in the end, that larvae nevertheless die under the care of males, opens up avenues for new lines of research. No one is, therefore, justified in claiming that they cannot do cutting-edge research due to lack of funds or facilities. And yet this is the almost universal excuse given by most people who should be doing good research but are not.

I am sometimes chastised for giving away the secret that cutting-edge research can be conducted with little or no money. The argument used against me is that if funders and politicians get wind of my claims, they will reduce funding for science. This imagined fear should not drive most of us to do expensive research just to prove that we need more money. Simply getting and spending more money should not be the source of satisfaction, prestige, or power. Different kinds of research need different levels of funding and different kinds of facilities. Research that doesn't require much money or facilities should not be made less fashionable. Indeed, we should all look for ways in which we get the most out of our research for the least amount of money.

One way to achieve and promote such behaviour is to devise metrics that divide research output by the money spent on it. Instead, today we flaunt grants received as an index of our success. This attitude may not be so easy to change as money is power, and the lure of large grants is irresistible to many. But at the very least, I wish to see that those who fail to get large research grants, for one reason or another, do not give up doing good science. Moreover, the distribution of grant wealth of researchers will inevitably be highly skewed with most of us having to make do with relatively small amounts of money. It is important for this large majority of researchers with relatively small grants, to nevertheless find ways of doing innovative research and disproving the belief that the quality of research is proportional to the grants received. And what about students who are yet largely outside the grant getting networks? Should they also be outside the knowledge-producing networks? In many cases, grant-free research may actually be easier, what with all the time saved by not having to write and defend grant proposals, battle the institutional bureaucracies to spend the money and with accounts and finance officers to comply with innumerable mindless rules. It might be good for researchers to begin their careers doing grant-free research and for grant earning scientists to deliberately plan and execute small research projects that require no money. We need to attach social prestige to grant-free or inexpensive research. We must introduce cost-effectiveness into the vocabulary and consciousness of scientists. The goal is not to reduce funding for science as a whole but to produce more out of the funding received and to continue to do cutting-edge research even when the funds have dried up.

It might be good for researchers to begin their careers doing grant-free research and for grant earning scientists to deliberately plan and execute small research projects that require no money. We need to attach social prestige to grant-free or inexpensive research.

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Suggested Reading

[1] P Burke, Fables of the bees: a case-study on views on nature and society, In: *Nature and Society in Historical Context*, (Eds.) M. Teich, R. Porter, and B. Gustafsson. Cambridge University Press, pp.112–123, 1997.

[2] M Cobb, Jan Swammerdam on social insects: A view from the seventeenth century, *Insectes Soc*., 49, pp.92-–97, 2002. Doi: 0020-1812/02/010092-05

[3] R Gadagkar, *Survival Strategies: Cooperation and Conflict in Animal Societies*, Harvard University Press, Cambridge, Massachusetts, USA and Universities Press, Hyderabad, India, 1997.

[4] R Gadagkar, *The Social Biology of Ropalidia marginata: Toward Understanding the Evolution of Eusociality*, Harvard University Press, Cambridge, Massachusetts, USA, 2001.

[5] R Gadagkar, How to design experiments in animal behaviour – 1. How wasps find their nests, *Resonance – journal of science education*, Vol.23, No.8, pp.871–884, 2018.

[6] R Sen and R Gadagkar,. Natural history and behaviour of the primitively eusocial wasp *Ropalidia marginata* (Hymenoptera: Vespidae): a comparison of the two sexes, *Journal of Natural History*, 44, pp.959—968,2010.

[7] R Sen and R Gadagkar, Males of the social wasp *Ropalidia marginata* can feed larvae, given an opportunity, *Animal Behavioiur*, 71, pp.345–350, 2006. doi:10.1016/j.anbehav.2005.04.022

[8] P Medawar, Is the scientific paper a fraud? *The Strange Case of the Spotted Mice and Other Classic Essays on Science*, Oxford University Press, UK, 1961.

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