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The story of caste and nutrition in an Indian paper wasp: it all began with logistic regression analysis

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Abstract

Only one or few individuals reproduce in eusocial insects such as ants, bees and wasps. The remaining function as sterile individuals that work for their colony. Such caste differentiation in highly eusocial species such as ants and honeybees is pre-imaginal, i.e., it occurs when the individuals are larvae. In primitively eusocial species such as many wasps and bees, caste differentiation is believed to be post-imaginal, i.e., it occurs after the individuals have become adults. Using the method of logistic regression analysis, and in collaboration with Prof. Anil Gore, we have shown that although social regulation in the adult stage is essential, there is nevertheless a pre-imaginal caste bias in the primitively eusocial Indian paper wasp *Ropalidia marginata*. Wasps that are well-fed as larvae develop into adults that feed more as adults and have a high probability of becoming queens. Conversely, wasps that are poorly fed as larvae develop into adults that feed less as adults and have a high probability of becoming workers. Thus, by controlling adult nutrition, we have succeeded in making selected wasps more selfish, i.e., more likely to revert from worker to queen roles either by replacing their queens or by leaving to start their own new colonies.

Keywords: *Altruism, Caste differentiation, Logistic regression analysis, Nutrition, Ropalidia marginata, Social Insects.*

1 The insect societies

Insect societies resemble human societies in many ways and may even be superior in some ways. Many species of insects, such as ants, bees, wasps,

I have reproduced some passages with slight modification from chapter 12 of (Gadagkar 2001).

and termites, organise themselves into colonies that remind us of our own society, because they display impressive levels of social organisation, coordination, communication, and division of labour. Insect societies, however, vary greatly in their levels of social organisation and the extent to which social life is obligatory. We refer to the most complex of these societies as eusocial, a term that means truly social.

In eusocial colonies, only one or a small number of individuals, whom we refer to as queens and kings, reproduce. The remaining individuals, whom we refer to as workers, labour for the colony's welfare, producing very few or no offspring of their own. Thus, all the tasks required for the colony's survival - building the nest, feeding and caring for the brood, guarding the nest and foraging - are the responsibility of the workers. We refer to groups of individuals who specialise in a set of tasks and perform them in preference or to the exclusion of other tasks, as castes. Thus, we refer to queens and workers as distinct castes (Wilson 1971).

2 Caste differentiation

It is helpful to recognise two further subdivisions among eusocial insects. The advanced or highly eusocial species maintain much larger colonies with thousands or even a million individuals and display striking morphological divergence between large and specialised queens and small workers specialised in their own way. On the other hand, the primitively eusocial species typically have small colonies with a hundred or fewer individuals and display no queen-worker morphological dimorphism. The advanced and primitively eusocial species show another important difference.

In advanced eusocial species, the differentiation of colony members into reproductive and worker castes takes place in the early larval (pre-imaginal) stages through a process of developmental regulation based on the nutritional environment of the larvae.

In primitively eusocial species, by contrast, caste differentiation takes place in the adult (post-imaginal) stage through a process of behavioural and social regulation. It is expected that social interactions in the adult stage permit only one or a small number of individuals to develop their ovaries and lay eggs while the ovarian development of the rest of the individuals remains suppressed. However, what newly eclosed individuals will actually do depends on the social and ecological conditions they find themselves in and, for temperate-zone species, also the time of the year (Hunt 2007).

Many species of bees and wasps are primitively eusocial. But are all eclosing individuals in primitively eusocial species really totipotent? Is caste determination entirely post-imaginal? This is one of the questions we set out to test many years ago using the Indian paper wasp.

3 The Indian paper wasp *Ropalidia Marginata*

The Indian paper wasp *Ropalidia marginata* (Gadagkar 2001) is a familiar inhabitant of gardens and undisturbed buildings all over peninsular India (Figure 1). It builds relatively small paper carton nests with characteristically hexagonal, honeycomb-like cells. A nest may be inhabited by one or, more often, by several adult wasps. All the adult wasps look identical, as expected for a primitively eusocial species.

Nevertheless, one and only one of them is the queen, the only individual who lays eggs and monopolises reproduction. The remaining adult females function as workers, building and cleaning the nest, feeding and caring for the larvae and foraging for food (insects and spiders) and building material (cellulose fibres that they scrape from plants), and occasionally water and nectar from flowers. All these materials are brought back to the nest, shared with their nestmates, and fed to the larvae.

4 The timing of caste determination

The ecology and social biology of *R. marginata* make the phenomenon of caste differentiation a particularly interesting one. Whether in the matter of readiness to replace a gradually weakening queen or one that has suddenly disappeared, or to participate in whatever competition goes on to be selected as an heir designate or even to take up an appropriate non-reproductive role, the timing of caste differentiation can have a crucial influence. Very early in my study of the Indian paper wasp, I began to wonder how one can investigate these questions.

Then, I made a serendipitous discovery that changed the course of my research with these infinitely fascinating wasps. I had collected a small colony of *R. marginata* in a little plastic box with a volume of about 200 ml. On this occasion, I was too tired to transfer the nest to a large laboratory cage, so I set the bottle on my desk and retired for the night. Arriving in the lab the following day, I found that while the old nest was still lying on the floor of the bottle, the wasps had initiated a new nest at the roof of the bottle, using the wood pulp scraped and recycled from the old nest. The queen was sitting on the new nest, and she had already laid a couple of eggs. The remaining wasps flew back and forth between the old nest lying below and the new nest on top. I now know that they will even cannibalise the larvae from the old nest and feed the larvae in the new nest.

This episode, resulting from my laziness, showed me how handy these wasps were and that I could maintain any number of small nests in small plastic bottles. I also soon discovered that virgin female wasps would readily build nests and lay eggs, although their eggs would develop only into sons.

This knowledge prepared the stage for me to test the null hypothesis that all R. marginata females are totipotent at eclosion and that caste is determined entirely in the adult stage. Thus, my null hypothesis was that all eclosing wasps are capable of laying eggs. I saw that one way to test the hypothesis was to isolate newly eclosed virgin wasps in individual plastic boxes and simulate the conditions required for nest initiation, i.e., just provide them with food and building material. I purchased large numbers of plastic boxes of the kind we use in the kitchen for storage. I placed the boxes upside down and fixed wire mesh windows on the walls for ventilation(Figure 2). I glued a small piece of plastic tubing on the inside of the cap to provide a few drops of honey and used small plastic Petri dishes to provide water in a piece of water-soaked sponge and some food. I experimented with different easily available food items and selected larvae of the rice moth *Corcyra cephalonica.* All these items could be obtained easily and in large quantities. We set up a separate culture of the rice moth using crushed jowar.

I then collected large *R. marginata* colonies, cleared them of all adult wasps, eggs and larvae and placed them in ventilated plastic boxes. Every morning, I looked for newly eclosed adult wasps, set free any eclosing males, and isolated each eclosing female in a plastic box prepared as described above. I made sure that every wasp had more food than it would consume so that food was not a limiting factor in their ability to develop their ovaries and lay eggs. My prediction was as follows. If caste determination was entirely post-imaginal, almost all the wasps tested should build nests, develop their ovaries and lay eggs. This is because they have not been subjected to any social interaction that might suppress their capacity for ovarian development. However, if caste determination is pre-imaginal, then most of the virgin wasps we test should have already been channelled into a worker developmental pathway and should be incapable of developing their ovaries and laying eggs and only very few individuals should develop their ovaries and lay eggs.

At about this time, a very able assistant C. Vinutha joined me and helped me in the day-to-day running of this massive experiment, and we were thus able to have a really large sample size - we tested 197 wasps! We terminated the experiment for each wasp on the day it laid its first egg or it died. It was indeed a massive operation to maintain such a large number of wasps, feed them, clean their boxes and keep records of their egg laying and dying. But the result was rewarding. Of the 197 wasps tested, 97 (49%) successfully built nests and laid at least one egg. We simply called these the 'egg layers'. The remaining 100 (51%) wasps died without doing so, and we referred to them as the 'non-egg-layers'(Table 1).

What sense could I make of this result, which was as intermediate and, thus, as indecisive as it could possibly be? Caste determination was not entirely pre-imaginal because we would not expect half the wasps to be channelled into a developmental pathway to make queens and the other half into a pathway to make workers - only a very small proportion of adult wasps need to be able to become fertile queens. The rest should be programmed to function as non-egg-laying workers. But caste determination was also not entirely post-imaginal because then I would have expected most of the wasps to develop their ovaries and lay eggs in the absence of social interactions that would have suppressed their ability to lay eggs.

I concluded, therefore, that there was a pre-imaginal caste bias such that about half the individuals were predisposed to become egg layers, and the other half were predisposed to become workers, leaving the fine-tuning of caste determination to social regulation in the adult stage. My interpretation was that the egg-layers in our experiment would have a high probability of capitalising on opportunities to become queens. By contrast, the non-egg-layers would have a low probability of capitalising on opportunities to become queens.

This was a most interesting conclusion, but I must confess I was not entirely happy. I had reached a dead-end, and that made me feel empty. I did not quite know how to go about analysing these data any further. And then, I met Anil Gore of the Department of Statistics at the University of Pune, now known as Savitribai Phule Pune University. Anil was rapidly becoming a friend, philosopher, and guide to many ecologists in India. His statistical expertise, combined with his passion for befriending ecologists and spending time with them to see their work first-hand, was truly inspiring. When I explained my work to him and presented my dilemma, he was so interested that I was a bit surprised. Then I discovered that he and his student Ashok Shanubhogue were developing computer programmes to deal precisely with my kind of data. It must be remembered, of course, that, in those days, ready-made statistical packages were not available, and people had to write their own computer programmes to do the analysis. But it had the merit that people really understood what they were doing. I was privileged to have them on board to make sense of our cryptic but profound result of 97:100. We used logistic regression analysis to model how the independent variables associated with the parent nest and the experimental wasps might influence the dependent binary variable, namely, whether a given wasp would become an egg-layer or a non-egg-layer.

In one model, where we tested nest properties for their potential correlation with the probability of wasps becoming egg layers, only one regression coefficient was significantly different from zero: the one associated with the number of empty cells (Table 2). In another model, where we tested variables associated with the wasps themselves for their potential association with the probability of becoming egg layers, the regression coefficient associated with adult feeding rate was highly significantly different from zero (Table 2). We concluded, therefore, that wasps eclosing on nests with large numbers of empty cells and those that feed well during their adult life have a high probability of becoming egg layers. In contrast, wasps eclosing on nests with small numbers of empty cells and those that feed poorly during their adult life have a low probability of becoming egglayers (Gadagkar et al. 1988).

These results were so intriguing that, despite the very large sample size they were based on, I felt it prudent to reconfirm them. I especially found the fact that almost exactly 50% of the wasps laid eggs rather uncanny. The fact that the number of empty cells was one of the significant predictors of the probability of egg-laying was even more intriguing. So, we repeated the experiment. In the second experiment, we tested 102 wasps and obtained 53 (52%) egg-layers and 49 (48%) non-egg-layers and reconfirmed all the results of the first experiment (Gadagkar et al. 1990). Now that all the results were reconfirmed, it was time to worry about what they might mean. So, what sense could we make of the possible roles of empty cells and feeding rates in influencing the probability that wasps would or would not develop their ovaries and lay eggs?

5 The possible significance of empty cells

The correlation between a high number of empty cells in the nest from which egg layers eclose and their high probability of becoming egg-layers was not easy to interpret. However, taking a cue from highly eusocial species and speculating that the queen may be involved in some way in biasing the caste of her brood, I constructed a conceptual model of caste biasing (Figure 3). In a normal, healthy nest, cells rarely remain empty. Queens usually lay eggs in cells vacated by pupae within hours of their becoming vacant. It is, therefore, reasonable to assume that the accumulation of empty cells in a nest, especially more than one or two cells that may conceivably be left empty by chance alone, is a strong indicator of the queen's declining influence. The queen's influence could decline owing to old age or poor health. But if R. marginata has indeed attained a certain level of sophistication in its mechanism of caste determination, then the queen's influence may also decline temporarily and in a programmed fashion during certain phases of the colony cycle that might be devoted to the production of future reproductives.

Whatever the cause of the queen's declining influence, our model postulated two consequences. One was the accumulation of empty cells, and the other was the production of adult wasps that are programmed to feed more and have a high probability of becoming egg layers. Conversely, other phases of the colony cycle might be devoted to producing a large worker force. During this worker production phase, we would expect the queen to exert a strong influence, leading to few or no empty cells and to the production of adult wasps programmed to feed less and have a low probability of becoming egg layers. We had no idea how the queen's weak influence could lead to the production of egg layers, and the queen's strong influence could lead to the production of non-egg layers. We, therefore, postulated two hypothetical processes, X and Y resulting from the queen's weak influence and strong influence, respectively, and hoped eventually to unravel X and Y.

6 The role of adult nutrition

The role of feeding rates, however, is easier to understand. It is reasonable to infer that high feeding rates permit wasps to obtain the required nutrition, develop their ovaries and lay eggs, and low feeding rates do not. But there is a conundrum here. We provided all wasps with ad libitum food. So, why should some wasps choose to eat less and become non-egg-layers? It could be the effect of the pre-imaginal caste bias, which I speculate channels some wasps into a developmental pathway that results in adults who feel more hungry, feed more and become egg-layers and other wasps into an alternate developmental pathway that result in adults who feel less hungry, eat less and become non-egg-layers. But what is the mechanism of pre-imaginal caste bias that channels developing larvae into these alternate developmental pathways?

7 The role of larval nutrition

The next course of action for me was obvious. Another experiment made even more tedious by the requirement that observations be made on the nests from which the experimental wasps eclose so that information could be obtained about the feeding rates of the experimental wasps when they were larvae.

Seetha Bhagavan, K. Chandrashekara, and C. Vinutha readily participated in this study. We now selected six new naturally occurring nests, made 4-6 days of behavioural observations on each of them, collected the nests, cleared them of adult wasps, eggs, and larvae, and isolated the eclosing female wasps into individual plastic boxes as before. Thus, we managed to test 87 wasps, and once again, close to half of them (47) became egg layers, while the remaining 40 became non-egg layers. From the data obtained during behavioural observations, we computed the number of times an average larva was fed per hour for each nest and used this value as the independent variable in the logistic regression model. The result was clear: the logistic regression coefficient associated with larval feeding rate was significant and positive (Table 3). Now, we could infer that those wasps that were well-fed as larvae appear to grow into adults who feel hungry, eat more and have a high probability of becoming egg layers. And individuals that are poorly fed as larvae seem to grow into adults who are not hungry, eat less as adults, and become non-egg layers (Gadagkar et al. 1991).

In the first experiment with 197 wasps, we had found another intriguing result. Among the 97 egg-layers, there was considerable variation in the time taken to lay eggs (mean $\pm$ sd $= 62 \pm 38$, range = 13-217 days) (Figure 4). In that study, we failed to detect any correlates of such variability in the time required to initiate egg-laying, but now we were also successful in discovering a correlate of the time taken by adults to start laying eggs. There was a weak but statistically significant negative correlation between the time taken by an adult wasp to attain reproductive maturity and start laying eggs and the rate at which they were fed when they were larvae (Figure 5). Thus, Larval nutrition seems to influence both forms of pre-imaginal caste bias: the differentiation into egg layers and non-egg layers and the further differentiation of the egg layers into early and late egg layers.

Thus, we deciphered the nature of the postulated processes X and Y in our model for pre-imaginal caste bias (Figure 3); X = high rate of larval feeding and Y = low rate of larval feeding. Now we had the complete story, or so we thought: individuals well-fed as larvae develop into adults that feel hungry, eat well, and become egg layers and perhaps early egg layers, and individuals poorly fed as larvae develop into adults that do not feel hungry, eat less, and become non-egg layers or late egg layers. But what is the correlation between the queen's influence and larval feeding rate, and, similarly, what is the correlation, if any, between the number of empty cells and larval feeding rate? These were challenging questions indeed.

However, I soon realised that an attractive hypothesis could potentially link all these variables. Imagine the following reasonable sequence of events in the life of a colony. New nests begin with relatively young and healthy queens that may leave few or no empty cells. Such new nests may also have a modest workforce that will be busy expanding the nest to match the queen's egg-laying rate. The food that is brought to the nest at this time may, therefore, be limited because few workers are foraging. Besides, the food brought to the nest must be shared with a relatively large number of larvae. Thus, there will be relatively less nourishment for the larvae, which will program them to become non-egg layers. In the course of time, the colony acquires a large workforce and also expends less effort in expanding the nest. In addition, the queen,either on account of old age and weakness or for the purpose of producing reproductives, may slow down her rate of egg-laying, causing an accumulation of empty cells and soon a reduction in the number of larvae to be fed, relative to the amount of food available. Larvae at this time may, therefore, be better nourished and hence be programmed to develop into egg layers. Such a scenario is consistent with what is known about the colony cycle (Jeanne 1972), variation in larval and adult nutrition through colony development (West-Eberhard 1969; Wilson 1971; Wheeler 1986; Hunt 1988; Hunt et al. 2003; Judd et al. 2015), and the postulated role of nutrition in social evolution (Pardi and Marino Piccioli 1970, 1981; Hunt 1984, 1990, 1991; Hunt et al. 1987, 1996; Rossi and Hunt 1988; Molina and O'Donnell 2008; Kapheim 2017)in many eusocial insects.

To complete the story and bring it to the present state of our knowledge, I will need to describe several more experiments. To do so, I will need to provide a lot of background information that is not mentioned above. However, since I have limited space, I will merely mention the remaining experiments without going into the details. In another experiment, we showed wasps could combine a worker strategy and queen strategy within their lives because the probability that they could revert to egg laying and start their own nests was not diminished on account of the work they had performed prior to that (Brahma et al. 2018). We had previously been plagued by the difficulty of observing the natural foundation of new nests by wasps leaving the nests of their birth. This is because we could not follow the wasps leaving their nests in nature, and in the laboratory cages, there was not enough space for them to be motivated to leave and start new nests. In the next experiment, we transplanted wasps in large walk-in cages and observed 29 nest foundations. This setup opened up the possibility of understanding who leaves the parent nest with whom and why. This experiment demonstrated that well-fed wasps were more likely to leave and start new nests (Brahma et al. 2019).

Finally, we were emboldened enough to attempt to make the wasps more selfish or less selfish by altering their nutritional levels.We hand fed the wasps (in addition to the provision of ad libitum food placed near the nest) in the experimental nest and provided only the ad libitum food in the control nests. When we did such experiments with nests in small cages with insufficient space, we found that well-fed wasps developed their ovaries better than control wasps and sat outside the nest as if expressing their desire to leave and start new nests (Shukla and Gadagkar, 2022). But when we repeated the experiment in the walk-in cages, we indeed found that excess feeding increased not only the probability of wasps leaving their nests of birth to start their own nests but also the probability that they would overthrow their queens and become new queens in their nests of birth (Krishnan et al. 2021).

8 Nutrition is the key to caste

The story of caste and nutrition in the Indian paper wasp *R. marginata* began with a paper we published with Anil Gore in 1988 (Gadagkar et al. 1988), showing that there is a pre-imaginal caste bias such that some individuals are more likely to become future queens and others more likely to become future workers. In the 34 years since that paper was published, we have performed a series of experiments to discover that wasps well-fed as larvae develop into larger-sized individuals who feel more hungry, consume more food, develop their ovaries better and faster, are more likely to become egg layers and are more likely to retain the potential to revert to the queen caste after spending time as a worker caste. Conversely, wasps poorly fed as larvae develop into smaller sized individuals, feel less hungry, consume less food, develop their ovaries poorly and slowly, have a low probability of becoming egg layers and a low potential of reverting to the queen caste after spending time as workers. Our saga of the story of caste and nutrition in the Indian paper wasp *R. marginata* ulminated in a study in 2021 (Krishnan et al. 2021) which showed that we could bias the caste of adult wasps at will by altering their nutritional status and making them more selfish (Richards 2021).

Like all good science, this line of research, while answering a fundamental question, opens up a major puzzle. If consuming more food can make the wasps into queens rather than workers, why don't they all feed more, at least in the experiment where we provide them with *ad libitum* food kept nearby, and why do they do so only when we hand feed them? This is especially intriguing because wasps of another primitively eusocial *Polistes fuscatus* seem to capitalise on the ad libitum food provided under laboratory-rearing conditions to be better nourished than their counterparts in field-reared natural colonies(Jandt et al. 2015). Clearly, we have to get back to work!

Table 1: Evidence for pre-imaginal caste bias.Numbers and (percentages) of egg layers and non-egg layers among eclosing wasps that were isolated from all adult conspecifics in three independent experiments. Data from (Gadagkar et al. 1988, 1990, 1991).

Expt no.	No. of wasps tested	No. of egg layers	No. of non-egg layers
1	197	97 (49%)	100 (51%)
2	102	53 (52%)	49 (48%)
3	87	47 (54%)	40 (46%)
Total	386	197 (51%)	189 (49%)

Table 2: Logistic regression analysis of determinants of probability of egg laying by females of *R. marginata*. Data (republished with permission of [The Royal Society (U.K.)], from [Gadagkar R, Vinutha C, Shanubhogue A, Gore A. P. (1988) Pre-Imaginal Biasing of Caste in a Primitively Eusocial Insect. Proc R Soc Lond B 233 (1271):175-189.]; permission conveyed through Copyright Clearance Center, Inc."

Variable	Estimated coefficient ($\underline{\beta}$)	S.E.	$\underline{z}$
Model 1: nest properties as determinants of the probability of egg laying by eclosing females			
Intercept	-0.1854	0.3335	-0.5558
No. of eggs	-0.0072	0.0155	-0.4641
No. of larvae	0.0060	0.0150	0.4020
No. of pupae	0.0101	0.0225	0.4472
No. of parasitised cells	-0.1536	0.1489	-1.0315
No. of empty cells	0.0519	0.0218	2.3845a
No. of males	0.1753	0.1771	0.9896
No. of females	-0.0111	0.0194	-0.5700

Variable	Estimated coefficient ($\underline{\beta}$)	S.E.	$\underline{z}$
Model 2: feeding rate and body size as determinants of the probability of egg laying			
Intercept	1.5631	4.1547	0.3762
Feeding rate	3.4993	1.2871	2.7188b
Interocular distance	- 6.4072	7.1170	-0.9003
Ocello-ocular distance	-11.7276	5.9464	-1.9722
Head width	1.2445	1.4517	0.8573
Head length	1.3271	1.4336	0.9257
Mesoscutellum width	- 1.0160	1.5312	-0.6635
Mesoscutellum length	1.1687	1.3327	0.8770
Wing length	- 0.2291	0.3216	-0.7125

a. $p < 0.02$, b. $p < 0.007$. c. $p < 0.05$.

Table 3: Logistic regression analysis of larval nutrition as a determinant of the probability of egg laying by eclosing females of *R. marginata*. Data republished with permission of [John Wiley and Sons], from [Gadagkar R, Bhagavan S, Chandrashekara K, Vinutha C (1991). The role of larval nutrition in pre-imaginal biasing of caste in the primitively eusocial wasp Ropalidia marginata (Hymenoptera: Vespidae). EcolEntomol 16 (4):435-440.]; permission conveyed through Copyright Clearance Center, Inc."

Variables	Estimated coefficient (β)	S.E.	Test statistic	$\underline{p}$
Intercept	-0.5612	0.3963	-1.4160	0.1556
No. of times an average larva is fed per hour	3.5462	1.6525	2.1459	0.0316

Figure 1: A large colony of the Indian paper wasp *Ropalidia marginata*, showing the hexagonal cells with eggs, larvae and pupae. Adult wasps are seen on the nest. One of the wasps is the queen but she cannot be distinguished by her morphology, from the rest who are the workers. Some of the wasps may be males but they cannot easily be distinguished unless we examine the faces. (Photo: Thresiamma Varghese).

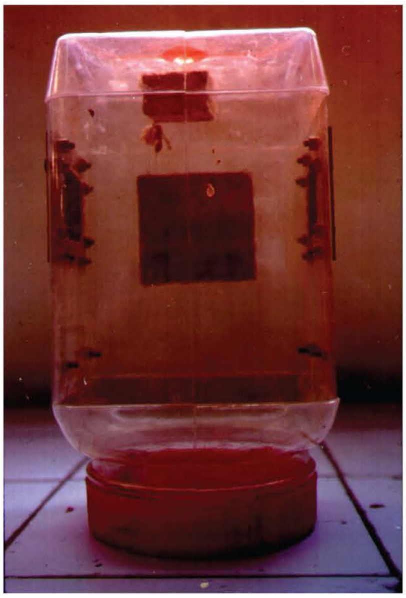

Figure 2: Plastic box (22 X 11 X 11 cm) used to keep individual wasps in the experiment.

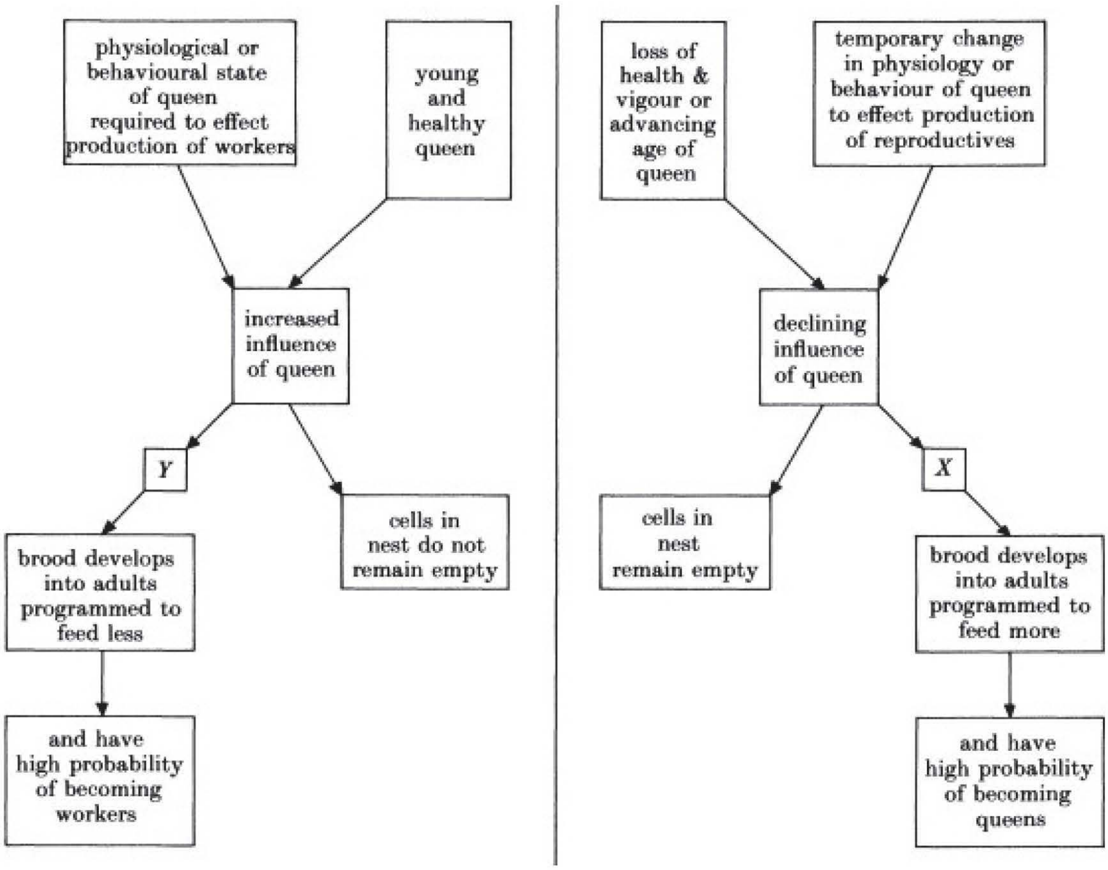

Figure 3: A conceptual model for pre-imaginal biasing of caste in the primitively eusocial wasp *R. marginata*. The left half of the figure depicts the set of processes that are expected to operate in nests that are in a phase of worker production whereas the right half depicts the set of processes that might operate in nests in the queen production phase. The numbers of empty cells are not hypothesized to be causal factors in caste determination (or biasing) but indirect consequences of the same set of processes that lead to caste determination. The rate of feeding by the adults, on the other hand, is postulated to be a link in the programming for caste determination. The underlying processes that are involved in such programming for caste determination, labelled X and Y. It is reproduced with permission of [The Royal Society (U.K.)], from [Gadagkar R, Vinutha C, Shanubhogue A, Gore AP (1988) Pre-Imaginal Biasing of Caste in a Primitively Eusocial Insect. Proc R Soc Lond B 233 (1271): 175-189.]; permission conveyed through Copyright Clearance Center, Inc.

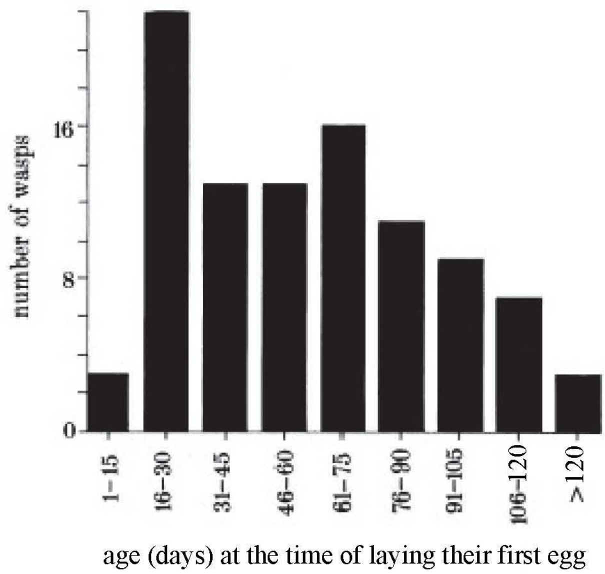

Figure 4: Distribution of wasps in different age classes at the time of laying their first egg.

In Figure 4, the distribution has a mean of 62 days, a standard deviation of 38 days and ranges from 13 to 217 days. It is reproduced with permission of [The Royal Society (U.K.)], from [Gadagkar R, Vinutha C, Shanubhogue A, Gore AP (1988) Pre-Imaginal Biasing of Caste in a Primitively Eusocial Insect. Proc R Soc Lond B 233 (1271):175-189.]; permission conveyed through Copyright Clearance Center, Inc.

In Figure 5 given below, there is a weak but statistically significant negative correlation between time taken by an animal to start laying eggs (= age at reproductive maturity) (shown as mean $\pm$ SD) and the rate at which larvae are fed in the nest from which they eclose. (Pearson product moment correlation $r = -0.42; df = 45; P < 0.01$.) The numbers on top of each bar represent sample sizes. It is reproduced with permission of [John Wiley and Sons], from [Gadagkar R., Bhagavan S, Chandrashekara K., Vinutha C. (1991). The role of larval nutrition in pre-imaginal biasing of caste in the primitively eusocial wasp Ropalidia marginata (Hymenoptera: Vespidae). Ecol Entomol 16 (4):435-440.]; permission conveyed through Copyright Clearance Center, Inc.

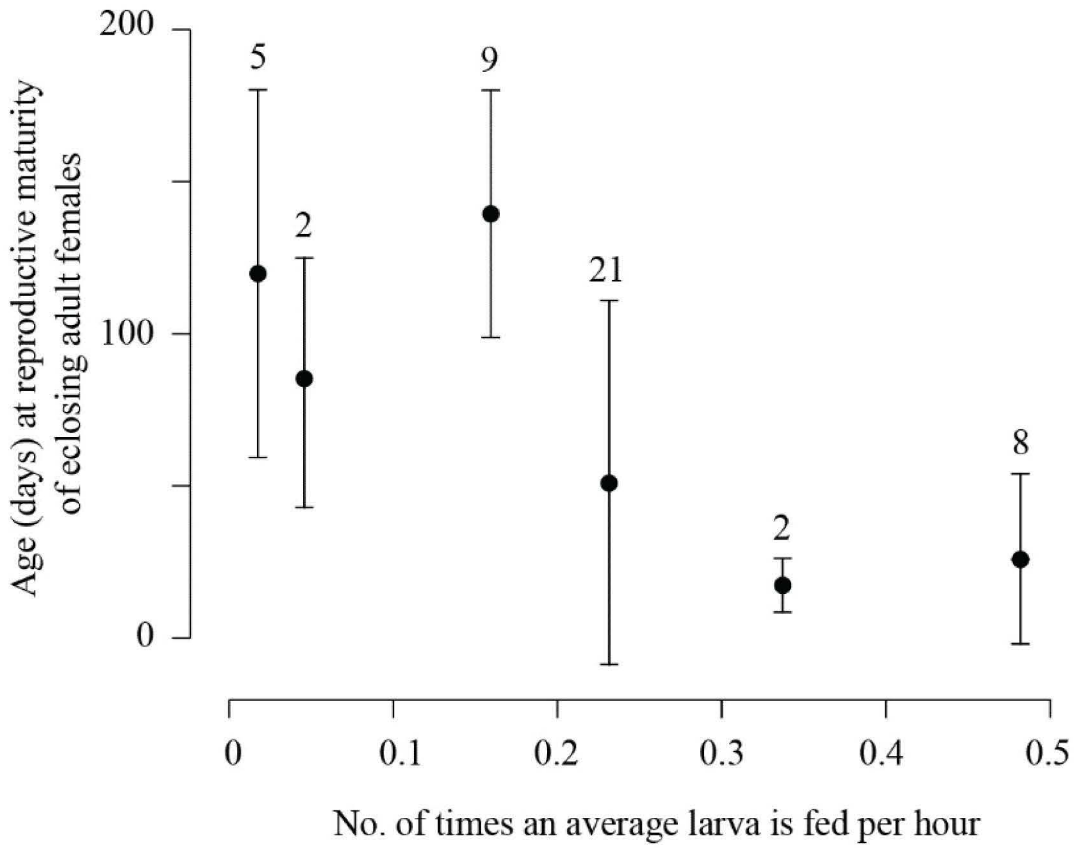

Figure 5

Acknowledgements

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