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scientific study**

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Complex behaviour in Social Wasps — Towards a scientific study

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ABSTRACT

Ethologists have traditionally avoided the question of animal intelligence. The justification put forward to support this attitude is that animal intelligence cannot be defined; many animals such as insects have too small brains for intelligence; and, that we do not have unequivocal examples of animal intelligence. This paper argues that these are misconceptions and that there is a strong case for the study of animal intelligence. A number of examples from the study of primitively eusocial wasp are given which strongly suggest the presence of a complex, intelligent behaviour.

INTRODUCTION

Do animals behave intelligently? Do they think about what they are doing? Are animals conscious of their actions? Such questions are seldom discussed by ethologists. There appears to be a strong taboo among ethologists to explore the animal mind in this fashion. Donald Griffin, until recently at the Rockefeller University, appears to be the lone crusader in the cause of the study of animal intelligence and thought processes [1–3]. His books provide a fascinating commentary of the complex and intelligent things that a wide variety of animals are capable of doing. In addition, his books provide an even more fascinating commentary of how ethologists seem to have a closed mind on the question of animal intelligence.

Why Study animal intelligence ?

Let me say briefly why I think that there is a strong case for the study of animal intelligence. This is best done by refuting the objections usually raised against this endeavour.

Definition

First is the question of definitions. How can we study animal intelligence, thinking and consciousness if we cannot even define these terms accurately? This criticism is a sure way of killing a field of enquiry even before it is born. No definition can satisfy everybody and hence our critics will consider themselves justified in preventing the study of these phenomena. Our response therefore should be that definitions are not so important and that there is no reason not to begin to study a complex phenomenon before we can write down a single cogent definition that meets everyone's approval. More importantly there are many satisfactory ways of describing what we wish to study. Call it Complex behaviour, Versatile behaviour, Intelligent behaviour, Thoughtful behaviour, Conscious behaviour, Flexible behaviour or simply Un-instinctive behaviour.

But in some ways it is easier to define what is not intelligent behaviour. The French naturalist Henry Fabre did a curious experiment with a digger wasp which builds burrows in the ground to rear its brood. Having built a burrow, it hunts a cricket meant to serve as food for its larva, places the paralysed cricket a small distance from the burrow and enters the burrow to inspect it and then returns to take the cricket in. When the wasp was inspecting the burrow, Fabre moved the cricket a little distance away from where the wasp had placed it. The wasp returned to take the cricket and discovered its absence. Finding the cricket soon enough, it once again placed it a small distance from the burrow and went back to inspect. Fabre of course shifted the position of the cricket again but the wasp once again discovered the cricket, placed it near the burrow and went back to inspect. After forty unsuccessful attempts to make the wasp take the cricket directly into the burrow without an intervening bout of burrow inspection, Fabre gave up in exasperation! Obviously the wasp was incapable of realising that since the burrow had been inspected so many times in the recent past that the cricket may now be directly be taken into it or that since it was simply not succeeding in taking the cricket into the burrow, it should try a little variation in its sequence of behaviours. This machine-like, unintelligent behaviour on the part of the digger wasp illustrates what is meant by intelligence, better than any definition of intelligence might do. The important point is that an intelligent animal should be able to respond to variable and unexpected stimuli in a manner that is variable but appropriate to a given context.

Small brains

Another familiar objection, especially to the possibility of intelligent behaviour in small animals such as insects is that their small brains cannot possibly provide for intelligent behaviour. There is little substance in this argument. It is being increasingly realised that it is not the size of

the brain or the number of neurons but the quality and quantity of connections that really matter. The small size of insect brains should not therefore deter us from investigating possible examples of intelligent behaviour on their part.

Animal–Human–Continuum

Almost all ethologists will admit that man was subject to the forces of natural selection, at least in the past, and few if any, will argue that there is a biological discontinuity between man and other animals. And yet the majority of ethologists implicitly create such a barrier when it comes to the question of intelligence. If man's body and basic behavioural capabilities have been shaped by the same forces of natural selection, it follows that animals could have evolved intelligence too.

Intelligent behaviour may have greater selective value

An appropriate principle that should guide us while considering the question of animal intelligence is that natural selection will select for stereotyped, instinctive behaviour if that serves the best interests of the animal in that context. Since Henry Fabres does not routinely displace crickets left near the nests of digger wasps, there is perhaps no selective value for intelligence of the kind that would enable the wasp to bypass burrow inspection in response to repeated displacement of its prey. Rigid hard-wired instinctive programming may thus be most appropriate for designing the behaviour of the wasp. On the other hand, if an animal has to respond in variable and novel ways to unpredictably changing environments, flexible, thoughtful and intelligent behaviour may be more appropriate for designing the behaviour of the wasp. A wasp so designed may be better able to cope with its environment and thus be selected over a more rigidly programmed robotic wasp. We should therefore expect intelligent and thoughtful behaviour on the part of animals when the context demands it.

Instinct—Intelligence continuum within each species

Another important fact that needs to be emphasised is that we might expect a continuum between highly rigid, hard-wired, instinctive behaviour and flexible, intelligent behaviour within the same organism, depending on the context. This must be obvious because we possess different levels of flexibility in many aspects of human behaviour too. An extreme example is that natural selection has used "reflexes" to programme even humans to react to certain stimuli when quick and invariant responses are of prime importance. On the other hand man has evolved to think and plan other aspects of his behaviour such as hunting and courtship.

Null Hypothesis

Die-hard critics may still argue that even if animals can be intelligent, how do we know or prove that they actually are. One answer to this is to remind the critics that our null hypothesis should be that we do not know whether an animal is intelligent and the alternate hypotheses that it is or is not intelligent. But most ethologists seem to give the impression that our null hypothesis is that animals are not intelligent. This is erroneous and it is important to bear that in mind because scientists, by convention try to minimise the error of wrongly rejecting a null hypothesis but do not worry too much about the error of wrongly accepting a null hypothesis. If our null hypothesis is that animals are not intelligent then we are heavily biased against the possibility of discovering intelligence.

Examples

But an even better way to counter this criticism is to carefully document examples of what appear to be complex, versatile, intelligent, thoughtful, conscious, flexible and uninstinctive behaviour on the part of animals. Griffin (1992) provides an impressive catalogue and I will not repeat any of them here. Instead, I will briefly describe some of my own observations on *Ropalidia marginata* and *Ropalidia cyathiformis*, two primitively eusocial wasps that I am fond of studying. These may sometimes be one-time serendipitous observations and it may not be possible to interpret them fully and perhaps even more difficult to confirm one's interpretation. Nevertheless they open up many questions and clearly point to the flexibility and complexity of the behaviour of the wasps.

The case of a colony fission

A colony of *R. cyathiformis* under observation in the month of April–May 1981 began to show a steep decline in both the number of adults present on the colony as well as the number of brood being reared. It was my fear that, as it often happens, the colony may be abandoned, bringing a premature end to my long-term study. Instead, what actually happened was far more interesting. On the evening of 31st May 1982, I had left the colony with 11 adult females, all individually marked with unique spots of coloured paint, as I always do with wasps under behavioural observations. On my arrival on the morning of 1st June 1982, I noticed with dismay that only 6 of the 11 females remained on the nest. It is not unusual for one or two wasps at a time to disappear from such colonies. But the disappearance of 5 wasps (nearly half the population) overnight aroused my suspicion. More than anything else, I did not want this colony to be abandoned and put an end to my study. I really wanted to find the missing wasps. That did not take long. I had

only to look around for a few minutes when, to my amazement, I found all the five missing wasps. Recall, that the wasps were all marked with unique spots of coloured paint, and I thus had no doubt that they were my wasps. What amazed more was that the 5 wasps were not just sitting there; they had a small nest of their own.

It then dawned upon me that these 5 wasps had deserted their original colony, perhaps revolting against the authority of the queen, and had decided to start their own new nest. It did not take me long to find out that OTBAA, one of the particularly aggressive individuals on the original nest, had become the queen in the new nest. My disappointment at the loss of half my wasps turned into great excitement. Clearly, half the population had deserted their declining colony and ventured out on their own. Perhaps the aggressive OTBAA had led the revolt and walked away with her followers. This even raised several questions in my mind. I could easily imagine that being dissatisfied with the state of the original colony, but not being able to dislodge the original queen BLATA and mend matters, OTBAA was forced to leave.

But what would be the consequence of this for the — *Rebels* that left and indeed for the — *Loyalists* that stayed back in the original colony. This was easy to find out. I simply continued my observations and included the new colony in my study. The result was remarkable. The colony fission turned out to be good for both the Rebels and the Loyalists. The Rebels did very well; their colony grew rapidly and they began to rear brood quite successfully. Even more remarkable, the Loyalists in the original colony also benefited. In sharp contrast to the declining condition of the colony before the fission, the situation improved and they too began to rear brood quite successfully. Clearly, the fission increased the fitness (or inclusive fitness) of both the Rebels and the Loyalists [4]. But why was there such a difference in the state of the nest before and after fission? It was my impression that there was too much aggression among the animals before fission. A quantitative analysis of the behaviour of the wasps before and after fission confirmed this suspicion. There were significantly higher rates of dominance behaviour per animal in the original colony before the fission, compared to the rates of dominance behaviour per animal either among the Loyalists or among the Rebels after fission.

An analysis of the pattern of aggression before the fission was even more instructive. Having witnessed the fission and identified the Loyalists and the Rebels, I could now go back to the behavioural data on these animals in my computer files and compare the behaviour of the Loyalists and the Rebels before the fission occurred. It turned out that the Loyalists were the real aggressors; they showed much more aggression towards the Rebels than the Rebels did towards the Loyalists. Indeed the Loyalists also appeared to have driven away a number of other animals

during April and May 1982 although I have no idea of the fate of these other animals. It is reasonable to conclude therefore that high rates of aggression reduced the efficiency of brood rearing before colony fission and the low rates of aggression, in both colonies after fission, allowed efficient brood rearing [4].

An examination of the caste and age-composition of the Loyalists and Rebels before the event of fission was equally interesting. By multivariate statistical analysis of time-activity budgets, we have previously demonstrated that both in *R. marginata* and in *R. cyathiformis*, adult female wasps can be classified into three behavioural castes or groups which we have called *Sitters*, *Fighters* and *Foragers* [5-7]. While there is little, if any, qualitative difference between different female wasps in a colony, there is clear-cut quantitative differentiation; Sitters spend more time sitting and grooming themselves than the Fighters and Foragers. Fighters show higher rates of dominance behaviour than Sitters and Foragers, and Foragers spend more time away from the nest and return more often with food or building material than do Sitters and Fighters. It also appears that unless there is a major perturbation like the death of the queen or an attack by the predatory wasp *Vespa tropica*, individual wasps "decide" to become Sitters, Fighters or Foragers early in life and stay that way for the rest of their lives. Equally important is the fact that the queens of *R. marginata* are almost always Sitters while the queens of *R. cyathiformis* are almost always Fighters.

At the time of the colony fission, the original queen BLATA (herself a Fighter, as per *R. cyathiformis* norms), who was 72 days old on the day of the fission, managed to retain with her, STNBA, a 58 day old Forager, OTYA, a 24 day old Forager, BLTDA, a 10 day old Sitter and BATRA and BATYA who were Sitters of age 5 and 3 days respectively. For the last two animals, the classification into the Sitter category may be subject to some error because all wasps behave like Sitters during the first week or so of their lives and only later differentiate into true Sitters, Fighters and Foragers. The Rebel queen OTBAA also herself a Fighter in the colony before fission, although only 19 days old on the day of the fission managed to take away 4 Foragers, STDGA, RTDGA, OTLBA, and BATSA, who were 58, 37, 17 and 8 days old respectively on the day of the fission. It appears therefore that the group of 11 wasps split about as evenly as might have been possible under the circumstances, an interpretation that is strengthened by the fact that behavioural castes of the wasps, both among the Loyalists and among the Rebels did not change after the fission. I imagine that no Sitter went with the Rebels because there was only one Sitter of any reasonable age, i.e. BLTDA [4].

But how did the Rebels manage to get together and leave at the same time and reach the same site to start a new nest? Was it a "snap" decision taken on the night of May 31st or was it "brewing" all

along? Was there some form of "groupism" well before the final event of fission? To investigate these questions, or atleast to begin to do so, we measured behavioural coordination within and between groups by computing Yule's association coefficients between pairs of wasps [4]. We then asked the question whether there was more coordination within groups than between groups. For instance, did wasps within a group synchronize their trips away from the nest and did Rebels and Loyalists avoid each other? The Rebels had high association coefficients amongst themselves. Of the 10 possible pairs of animals among 5 Rebels (excluding 5 self-pairs and 10 repeats), 5 pairs had the highest possible association of +1 while the mean for the 10 pairs was 0.69. Monte-Carlo simulations show that this value could not have been obtained by chance and that it is statistically significant at $p < 0.01$. Similarly, the Loyalists amongst themselves also had a positive association coefficient although this was not statistically significant. In contrast, when we chose pairs of wasps such that one was a Loyalist and the other a Rebel, of the 15 possible pairs with 6 Loyalists and 5 Rebels, 4 pairs had the lowest possible value of -1 and the mean of the 30 pairs was -0.26. This also could not have been obtained by chance and is statistically significant at $p < 0.05$. These results demonstrate that the wasps had differentiated into two groups well before the fission with the Loyalists and Rebels behaving as two coordinated groups and avoiding each other [4]. The results also suggest that the wasps were capable of individual recognition and had some way of deciding when to leave and where to go.

Do wasps form alliances ?

In early 1985 I had a nest under observation for the purpose of removing the queen to see who would be next queen; indeed my long-term goal was to predict who the next queen would be. The behaviour of two of the wasps was particularly interesting. RT was very aggressive and particularly so towards DBA. She would harass DBA so often and for such prolonged periods of time that on several occasions I noticed that the queen would intervene. The queen would actually climb on the grappling mass of RT and DBA and separate them. This was clearly of great help to DBA who was no match for RT. I got the distinct impression that DBA in turn was not only trying to avoid RT but was also trying to appease the queen.

The most dramatic example of this occurred one day when DBA returned with food but before she could land on the nest, RT noticed this and poised herself to grab the food from DBA. It appeared that DBA did not want to give the food to RT. It also appeared that she wanted to give the food to the queen. But the queen was looking the other way and did not notice DBA arrive. DBA's response was very

interesting She landed on the leaf on which the nest was built about 2 cms away from the nest—something that returning foragers seldom do—they mostly alight on the nest. Having done that, DBA sitting on the leaf, and RT sitting on the nest, went through what might be called a war of attrition for over 5 minutes; DBA would attempt to get on the nest but RT would block her way and try to grab the food. Not having succeeded either in attracting the attention of the queen or in climbing onto the nest without losing the food load to RT, DBA now simply walked around the nest and came in full view of the queen. The queen seemed to immediately sense what was going on. She let DBA climb onto the nest and took the food load from her mouth but at the same time RT pounced on DBA and bit her, but before too long, DBA managed to escape from the clutches of RT and fly away.

This episode, dramatic as it already was, assumed even greater significance by the rather unusual turn of events after I removed the queen. Clearly, RT was the next most dominant animal and I had little doubt she would be the next queen after I removed the present one. But to my surprise, it was DBA who became the next queen, in spite of RT's presence. Indeed, RT stayed on for over a month after DBA took over but I cannot help describe her behaviour as "sulking"—she would do nothing at all except occasionally take some food from one of the foragers. She did not participate in any nest activity, quite in contrast to her earlier behaviour. Even Sitters do a fair amount of intranidal work but not RT, who therefore could not be classified as either a Sitter, a Fighter or a Forager by the multivariate techniques that I normally use—she was a clear outlier [7].

Why was RT so aggressive towards DBA compared to her behaviour towards other animals? Why was the queen so "considerate" towards DBA? Was there some kind of alliance between DBA and the queen? Did this in any way influence DBA's becoming the next queen when I removed the original queen, even though RT was higher in the dominance hierarchy? Since what I have described is the result of one chance observation, I will not pretend to answer these questions but clearly they are pointers to the potential flexibility and complexity of the behaviour of the wasps and to the possibility of alliances among them.

Do workers choose their queens ?

During a similar queen-removal experiment with *R. cyathiformis*, I once had a situation when there were two contenders, as it were to replace the existing queen. These were DBT and OT both more or less equally dominant. When I removed the queen on the 9th of March 1985, for whatever reason, DBT took over the place of the queen and OT promptly left the colony. However, DBT apparently was not a very

“good” queen. All the other wasps stopped foraging and began to simply sit on the nest. Even when they did go out, they always returned with nothing. Clearly DBT had eggs to lay because she began to cannibalize on existing eggs to make room for her to lay her own, as no one would bring building material or build new cells for her. Eventually, other wasps began cannibalizing on brood too and I was afraid that the colony would be abandoned. I was amazed to notice however, that OT had not quite given up. She would occasionally come back, as if to check on how DBT was doing. She would never spend the night on the nest but would only visit occasionally. By about the 20th of March, OT returned for good and DBT left. A pity that I was not there to witness their meeting! Now the behaviour of the rest of the wasps was dramatically altered. They began to work — they foraged, brought food, fed larvae, extended the walls of the cells of the growing larvae and even brought building material and built new cells for their new queen OT to lay eggs in.

The story does not quite end there. DBT also, it turned out, had not quite left the nest. She would also come from time to time and visit, as if to see how her rival, OT was doing. After a few days, DBT decided to rejoin the nest but not before a great deal of hostility by the resident wasps. DBT had to spend nearly a whole day and be subordinated by several residents before she was accepted back. It is the striking difference in the behaviour of the same set of wasps during the reign of two different queens that is most suggestive. Once again, it not only points to their capacity for individual recognition but also suggests that they are able to modify their behaviour based on such recognition. Why did the wasps not cooperate with DBT when she first took over as the queen? If she was simply not good enough to be a queen, why did she succeed in the first place, especially in the presence of OT? Again, I will not pretend to answer these questions but even without answers, the questions themselves provide evidence of the complexity and flexibility of the behaviour of these wasps.

Do wasps evaluate their chances of becoming queens ?

Several aspects of the behaviour of the wasps suggest that wasps constantly evaluate their chances of becoming queens. Indeed, I have argued that neither the opportunity to raise brood with particularly high genetic relatedness to themselves nor parental manipulation explains why workers in *R. marginata* work but that they seem to work because they are *hopeful queens*, awaiting opportunities to reproduce. It would be most appropriate therefore if wasps have evolved ways of assessing their chances of becoming queens under various circumstances and modulating their behaviour accordingly. Sometimes, but not always, wasps work for many days in their natal nests before they leave to start their own

nests. Could it be that their first option was to become queens in their natal nests, but since that did not happen, they chose the next option namely, starting their own nests? While wasps are usually very aggressive to non nestmate intruders, sometimes they allow foreign wasps to enter and join their colony. Could it be that some intruders are more acceptable than others? Sometimes wasps will cooperate with unrelated individuals to start new nests. Could it be that wasps are measuring their chances of becoming queens in the group they are to nest with? If they are, then it seems far more likely that their ability to do so comes from flexible, intelligent, thoughtful behaviour rather than hard-wired, instinctive behaviour. Indeed, I would argue that such cognitive abilities of the wasps may have played an important role in the evolution of eusociality. If the origin of eusociality depended not only on assessment of genetic relatedness values but on the ability of insects to engage in complex mutualistic interaction, as our research appears to show, cognitive abilities and their role in social evolution should receive special attention rather than be completely ignored, as is presently the case.

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