

Life, Mind and Consciousness

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Are Animals Conscious of Their Actions?

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Abstract

It is of course possible to define consciousness in a manner that automatically excludes animals from consideration. But it is also possible to define consciousness in a manner that makes it possible, at least in principle, for animals also to be conscious of their actions; only such a definition interests me. The main reason for my prejudice comes from my study of the ants, bees and wasps that live in complex societies with social organization, communication, division of labour and an ability to exploit the environment, that parallel human societies in many ways. In this talk I will describe some of the especially impressive features of insect societies and let the audience decide for itself whether the animals I deal with can be thought of as being conscious of their actions. At the outset, I wish to thank the authorities of The Ramakrishna Mission Institute for Culture and Prof. Samir Bhattacharya for inviting me to participate in this fascinating international seminar on Life, Mind and Consciousness. I feel honoured to be in the company of such a distinguished group of scholars and I feel especially honoured because I am here to represent $n-1$ species of animals, where n has been estimated to be upwards of

10 million! But I am handicapped, first, because I have to follow the most eloquent and erudite presentation by Swami Jitatmanandaji and second because most of us have got used to regarding non-human animals (hereafter referred to simply as animals) as significantly 'inferior' to humans. I would, therefore, like to begin with a caveat. Although I do not have a precise definition of consciousness, I have my own prejudice about possible definitions. I realise that it is easily possible, and perhaps even convenient, to define consciousness in a manner that automatically excludes animals from consideration. However, such a definition does not interest me. I believe that it is also possible to define consciousness in a manner that makes it possible, at least in principle, for animals also to be conscious of their actions; only such a definition interests me.

The gene-culture continuum

One reason for my prejudice for a definition of consciousness that admits animals into its fold is what one might call, the gene-culture continuum. The history of ethology (the study of animal behaviour) is replete with controversies of instinct versus learning or, nature versus nurture. Instinct is defined as complex, inborn, un-learned, predictable, species-specific behaviour. The early part of the 20th century witnessed the peak of this controversy when a school of American psychologists who called themselves Behaviourists sought to deny the existence of instinct altogether and attempted to explain all behaviour of animals by learning alone. On the other hand, classical ethologists (mostly in Europe), while not denying the role of learning, found incontrovertible evidence of instinct in virtually every organism they investigated. By about the mid-1960's, the air was

cleared somewhat and most reasonable people admitted that animal behaviour was some complex mixture of instinct and learning. Today we have come a long way and recognise a whole series of intermediate steps from Genes to Culture, indeed, we recognise a gene-culture continuum. Recent research has provided evidence for the genetic basis of such complex behaviours as division of labour in honey bees and migratory routes in birds, to take just two examples, but this has not diminished our appreciation of the role of learning. Our understanding of the abilities of animals to learn, innovate and even teach each other has expanded even more impressively but again, that has by no means taken away our respect for instinct. Like in all controversies, hind-sight makes it so obvious that the truth lies somewhere between the two extremes so that today we have no difficulty in seeing a gene-culture continuum.

At one extreme, consider the simplest living organism, perhaps the bacteriophage (a virus that infects bacteria), whose 'behaviour' (it does not exhibit much of what one might call behaviour, but shows enough to get by in the world) is almost entirely governed by the handful of genes that it carries along as it jumps from one host bacterium to another. One can hardly expect anything more complex than genetically programmed 'instinct' in the life of a bacteriophage. Nevertheless, even at this simplest threshold of life, what the phage has 'learned' while in one host bacterium by way of modification of the nucleotide bases of its DNA is known to influence its behaviour in the next host bacterium. At the other extreme is man, the cultural animal, who can learn such abstruse skills as matrix algebra (which can hardly have an instinctive component) or indeed can learn to practice such

remarkable habits as smoking marijuana (which can hardly be thought of as having selective value). Nevertheless, even man shows unmistakable signs of the genetic basis of behaviour including in such complex contexts as dominance, depression, appreciation of music and the tendency towards certain forms of mental illness. One can imagine a series of intermediate steps in the gene-culture continuum: reflexes, instinct, imprinting, programmed learning, flexible learning, innovation, cultural transmission and teaching and consciousness. It would be incorrect to imagine that these intermediate steps occur in pure form in any organism. Instead, some complicated mixture of several steps combine to produce the behavioural repertoire of each species. For instance, one can see clear examples of all of these in man and equally clear examples of many of these in a variety of 'lower' and 'higher' animals. Just as there is no *a priori* reason to doubt the existence of reflexes and instinct in humans there is no *a priori* reason to doubt the existence of culture and consciousness in animals.

Behavioural complexity of insect societies

A second reason for my prejudice comes from my experience of studying insect societies such as those of ants, bees and wasps which are not only most impressively complex but have unmistakable parallels with human societies. I will only have space to give a few examples.

The honey-bees

Honey-bees live in populous colonies consisting of tens of thousands of bees. Each colony consists of a single fertile, mated queen bee, a small number of males (also called drones) while the rest are sterile

female worker bees. The queen does little more than lay eggs and produce chemical messengers called pheromones that help regulate the functioning of the workers. The drones stay in the colony but do not participate in any domestic duties; they merely mate with virgin queens from other colonies and die. All domestic work is performed by the workers who build and clean the nest, nurse the brood, process food, guard the nest and also go out of the nest to forage for nectar and pollen. These various duties are all performed by most workers within their lifespans of about six weeks, in a sequential manner, switching from one task to another as they grow older. The sequence in which worker bees perform their duties is not random. It is highly predictable and clearly adaptive both for the individual bees as well as for their colonies. Worker bees behave as if they know their age and also know what bees of that age should do. Even more impressively, bees can also do what is inappropriate for their age, if bees of certain ages are missing from the colony so that they fill in for the missing bees. For instance, some young bees forage at an abnormally young age when older bees are missing and these are termed 'precocious foragers'. Similarly some older bees nurse larvae at an abnormally old age when younger bees are missing and these are termed 'over-aged nurses'. It is easy to create precocious foragers and over-aged nurses by simply removing old and young bees respectively from the colony. Worker bees appear to choose tasks that they are good at and those that the colony needs at any given time. How each worker bee knows what task it should perform at any given time is a question that is being vigorously investigated. This is of great interest not only to honey-bee researchers but

also to those who wish to run efficient human organizations, be it a factory or software company.

Without the aid of learning, trial and error or a leader, worker bees perform a number of amazing tasks to perfection. With the wax that they secrete from their wax glands, worker bees make large combs of wax with perfectly hexagonal cells which are then used either for rearing brood or for storing brood. Thousands of larvae are fed several times a day with a mixture of pollen, honey and oral secretions, the quality and quantity of food being adjusted according to the age, sex and caste (queen or worker) of the larvae. Queen-destined larvae are given a special royal jelly early in life which puts them on to a different developmental pathway leading to altered gene expression, hormone production and morphological and physiological development suitable for queens rather than workers. Dead bees are recognised by the smell they emit so that undertaker bees remove them. Relatively older workers function as guard bees, smelling all bees at the hive entrance and permitting only nest-mates to enter.

The oldest workers venture out of the colony in search of nectar and pollen. A successful forager that returns to the colony attracts the attention of her sisters by means of a chemical she releases upon arrival. This usually ensures for her an attentive audience to begin her dance. The forager, who alone possesses information on the location of food, performs either a round dance or a waggle dance. During a round dance the bee runs in small circles, often alternating between clockwise and counter-clockwise directions. During the waggle dance, the forager waggles her body from side to side several times per second while running in a straight line, and then returns to the starting point without waggling her body, in a clockwise

or counter-clockwise direction. She then repeats the waggle run, thus inscribing a figure of eight. The round dance is performed if the food is within 100 m or so of the colony and the waggle dance is performed if the food is located beyond that. The round dance appears to provide no more information than that there is food close by. But the waggle dance has been shown to convey information about the distance between the colony and the food, the direction in which the food source is located as well as an indication of how much food is to be expected. The dancer also carries the smell of the pollen and/or nectar that she has recently encountered and that adds to the knowledge of the potential recruits, both during the round dances as well as during the waggle dances. The direction of the waggle run contains information about the direction of the food. Most species of honey-bees dance on the vertical surface of the nest which may be built inside a dark cavity. Hence bees use gravity and not the sun as the reference point while dancing. For this bees have to transform the angle between the sun (or, to be more precise, the sun's azimuth, meaning its projection on the horizon), the food, and their nest, into an angle with respect to the vertical. The number of figure eight circuits made per unit time and the duration of each waggle run indicate the distance between the nest and the food source. There are good reasons to call this communication system of the honey bee a language.

Firstly, the bee language conveys information about something at great distance and not visible at the time of communication. The notations are arbitrary; 'up' means in the direction of the sun because that is what the bees seem to have 'agreed' upon, but it could as well have been that 'down' means in the direction of the sun. Even more

interestingly, the bee dance language also appears to have dialects. There are slightly different calibrations of the figure of eight circuit duration with distance, depending on the race of bees one is looking at. No other animal species with the exception of man is known to have developed a system of communication comparable to the language of honey-bees.

Amazing as it is, the honey-bee dance language is not nearly as amazing as the sting of the bee. The sting of the worker bee is armed with barbs pointing away from its tip so that when firmly lodged in the victim's skin, it cannot be withdrawn. When the bee attempts to fly away after stinging, the sting, the poison gland, and a part of its digestive system are torn away and left hanging on the victim. This of course ensures efficient delivery of venom into the victim's body as the poison gland keeps pumping venom for some 30 to 60 seconds after the bee has flown away. However for the bee, stinging is an act of suicide in an attempt to protect its colony, an act of supreme sacrifice or altruism.

Ants and Agriculture

Human agriculture which is believed to have originated some 10,000 years ago has rightly been considered the most important development in the history of our species. Virtually all the plants which we consume today are derived from cultivars that have been bred and modified by humans for thousands of years. There has also been extensive exchange of cultivated crops from one part of the globe to another. While consuming plants and their products, we tend to forget that the cultivation of coffee originated in Ethiopia, that of tobacco around Mexico, tomato and potato in south America, rice in south-east Asia and so on. The impact of agriculture on the further development of human societies has been profound—

high rates of population growth, urbanization and economic surpluses all of which were prerequisites for the development of modern civilization, with its science, art, culture, religion, philosophy ...

Impressive as all these are, our achievements are surely humbled by the lowly ants which appear to have invented agriculture, and as we shall see below, a fairly sophisticated type of agriculture, almost 50 million years before we did. At least three different groups of insects practise the habit of culturing and eating fungi. They are, some ants from the new world, some termites from the old world and certain wood-boring beetles. While the beetles in this group are few and not of comparable importance, the fungus growing ants in the new world, and termites in the old world, are ecologically very dominant. With a few exceptions, all fungus growing ants are also leafcutters—they cut pieces of leaves, bring them to the nest and use them as substrata to grow fungi. The ants derive their nutrition only from the fungi so grown and not from the leaves themselves. There are today some 200 species of ants which do not know any lifestyle other than fungus farming. Because of their ecological dominance and their insatiable hunger for leaves, leafcutter ants are of major pests in the new world. These ants can devastate forests and agriculture alike—they may maintain ten or more colonies per hectare and a million or more individuals per colony. Where they occur, the leafcutter ants consume more vegetation than any other group of animals. Not surprisingly, many Latin American countries have passed national laws declaring leafcutter ants as 'plague animals'.

Like in the humans, the advent of agriculture appears to have significantly affected the evolution of leafcutter ants. Today the leafcutter ants are among the

most advanced and sophisticated social insects. As may be imagined, the process of fungus cultivation is a complicated business. In the field, leaves are cut to a size that is most convenient for an ant to carry them back. In the nest the leaf fragments are further cut into pieces 1-2 mm in diameter. Then the ants apply some oral secretions to the leaves and inoculate the fragments by plucking tufts of fungal mycelia from their garden. The ants maintain a pure culture of the fungus of their choice and prevent bacteria and other fungi from contaminating their pure cultures. Growing pure cultures of some of these fungi in the laboratory has proved difficult or impossible for us. How the ants achieve this remarkable feat remains poorly understood. Not surprisingly, they manure their fungus gardens with their own faecal pellets. When a new colony is to be founded, the new queen receives a 'dowry' from her mother's nest—a tuft mycelia carried in her mandibles! Thus these ants appear to have asexually propagated certain species of fungi for millions of years.

What kind of fungi do these ants cultivate? Do all ants cultivate the same type of fungi? As in the case of human beings, have there been multiple, independent events of cultivation of wild species? Like humans, do the ants exchange cultivars among themselves? Until recently it was not easy to answer any of these questions. Today, with the advent of powerful DNA technology, answers to many of these questions can be attempted. In one study, ant researchers and molecular biologists joined forces to do precisely this. First, they collected 553 samples of fungi from the fungus gardens of 7 genera of ants. Next they compared variable regions in the DNA of each of these samples and also sequenced and compared portions of two genes from 25 free-living and 57 ant-cultivated fungi. Their results suggest that there may have been at least five different

independent origins of fungal cultivation by ants, rather than a single event as was previously supposed. Even more interestingly, their results suggest that ants occasionally exchange fungal cultivars among themselves so that different nests of the same species of ants may contain different cultivars. Whether the ants deliberately borrow fungal cultivars from their neighbours or whether the horizontal transfers occur accidentally is however not known. Perhaps the most fascinating question to arise out of these findings concerns the impact of agriculture, including that of economic surplus thus generated, on their social and cultural lives.

A primitive wasp society

What are primitively eusocial wasps? I study social wasps, mainly two species called *Ropalidia marginata* and *Ropalidia cyathiformis*. These wasps are called paper wasps as they build their nests from paper which they themselves manufacture from cellulose fibres scraped from plants. The nests are like honeycombs in having hexagonal cells but the nests are much smaller (rarely exceeding 500 cells) and so are the number of wasps (rarely exceeding 100) on the colony. This makes it easy for me to mark every individual wasp and make detailed observations on their behaviour, their interactions with other members of the colony and their contribution to the welfare of the colony. There are many interesting differences between these wasps and advanced insect societies such as ants and honey bees. Unlike the latter, these wasp colonies do not have a well-differentiated queen. The wasps in a colony all look alike. However, only one individual in *R. marginata* and one or a small number of individuals in *R. cyathiformis* function as queens at any given time.

The wasps in a colony fight and the winner usually becomes the next queen in the same colony but only for a while as she may also be challenged and driven away by one of the others who then becomes the next queen and so on. The individuals who are not queens at any given time act as workers—they do not reproduce but instead, build the nest, forage for food and care for the brood. I mark the wasps with unique spots of quick drying coloured paints of different colours so that I know each wasp from the other. In many cases I simply refer to a wasp by the colour of the paint I have given it like Red, Orange, and Blue.

New nests are started by one or a group of female wasps. If it is a single foundress colony, the foundress acts both as the queen and worker and manages all by herself to bring her eggs to adulthood. In a multiple foundress nest, one of the foundresses assumes the role of queen while the others assume the roles of workers. The queen lays eggs in the cells of the nest and when the eggs hatch into larvae they are fed on a diet of spiders, bugs and caterpillars and occasionally some nectar by the queen herself in single foundress nests and by workers in multiple foundress nests. Not all workers work to the same extent or do exactly the same things although they are quite flexible about what they will do in an emergency. Under normal conditions, some of the workers take on most of the burden of going out of the colony in search of food and building material. We call these the Foragers. Others specialize in staying home and working on the nest and on the brood. Even among these, some are more aggressive towards other members of the colony and we naturally call these the Fighters. The remaining also work on the nest but are relatively quiet wasps and spend more time just sitting and grooming themselves and we call them

Sitters. As the larvae complete development, they pupate in the same cell and undergo metamorphosis. The entire process of maturing from an egg into an adult wasp may take about two months. If the wasp emerging from the pupa is a male, he will stay on the nest for about a week in *R. marginata* and then leave to lead a nomadic life, mate with some foraging female wasp and die. In *R. cyathiformis*, the males spend their whole lives in the colony and go out from time to time apparently to mate with wasps from other colonies. Mating never takes place at the nest. In either species the males take no part in any aspect of social life; they do not forage, feed larvae or build. The wasp society like all bee and ant societies is a female society—a feminine monarchy.

If the emerging wasp is a female, she appears to have a number of options open to her. She may leave to start a new nest all by herself, she may leave with a group of females or she may join females from other colonies to start a new nest. Alternatively, she may stay back and assume the role of a worker in the colony of her birth. Finally, she may stay back, work for some time, and eventually drive away the queen and take charge as the next queen in the colony of her birth. Of course such a power struggle may also take place among the cofoundresses in a new colony so that one foundress may replace another even before producing any offspring.

Now why do we call this a primitive society? The social ants, bees and wasps have evolved from solitary ancestors. In the transition from solitary to social life, it is reasonable to think that species would have gone through different stages of (a) nesting together without much interaction, (b) nesting together with interaction and some division of labour and finally (c) obligate

nesting together with one or a small number of morphologically specialized queens completely suppressing reproduction by the rest of the colony members. In *R. marginata* and *R. cyathiformis*, the wasps nest together, cooperate in nest building and brood care and show some division of labour. However, there is no morphologically differentiated queen incapable of performing the role of worker, and most workers can become queens if the opportunity presents itself. Besides, almost any wasp can start a nest and bring up her offspring by herself without participating in social life. Compared to the ants and honey bees, *R. marginata* and *R. cyathiformis* constitute a less advanced or more primitive insect society. I and my students have studied these wasps for over 20 years and gained considerable insight into the problem of the evolution of social behaviour in insects. I will not describe these more technical studies here. Instead I will describe some early observation that I made on *Ropalidia cyathiformis*, which have never been incorporated into any of our formal analyses. This is because these observations are so radical and point so unmistakably to the possibility of flexible, intelligent and perhaps conscious behaviour of the wasps.

Wasp politics?

In April 1981 I was studying a colony of *Ropalidia cyathiformis*. The colony began to show a steep decline in both the number of adults present on the colony as well as the 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 me 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 Orange, 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 on their own. Perhaps the aggressive Orange had led the revolt and walked away with her followers. This event 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 and mend matters, Orange 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 of both the Rebels and the Loyalists. But why was there such a difference in the level of cooperation before and after fission? It was my impression that there was too much aggression on the nest before fission. A quantitative analysis of the behaviour of the wasps before and after fission confirmed this suspicion. 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 individuals 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 individuals during April and May 1982 although I have no idea of the fate of these other individuals. It is reasonable to conclude the afore that high rates of aggression reflect a high degree of conflict which reduced the efficiency of brood rearing, before colony fission; and the low rates of aggression, in both colonies after fission, reflect a high degree of

cooperation which allowed efficient brood rearing.

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 even before the final event of fission? To investigate these questions we measured behavioural coordination within and between sub-groups (Rebels and Loyalists) using a mathematical index called the association coefficient. We then asked the question whether there was more coordination within sub-groups than between sub-groups. For instance, did wasps within a sub-group synchronize their trips away from the nest and did Rebels and Loyalists avoid each other? It turned out that the Rebels had high association coefficients among themselves. Similarly, the Loyalists amongst themselves also had a positive association coefficients although this was not as high as the value among the Rebels. In contrast, Rebels and Loyalists had a negative association with each other. This suggests that the wasps had differentiated into two sub-groups well before the fission, with the Loyalists and Rebels behaving as two coordinated sub-groups and avoiding each other. The wasps must, therefore, have been capable of individual recognition and have had some way of deciding when to leave and where to go.

Do wasps form alliances?

In early 1985 I had another nest under observation for the purpose of removing the queen to see who would be the 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. Red was very aggressive and particularly so towards Blue. She would harass Blue 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 Red and Blue and separate them. This was clearly of great help to Blue who was no match for Red. I got the distinct impression that Blue in turn was not only trying to avoid Red but was also trying to appease the queen.

The most dramatic example of this occurred one day when Blue returned with food but before she could land on the nest, Red noticed this and poised herself to grab the food from Blue. It appeared that Blue did not want to give the food to Red. 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 Blue arrive. Blue's response was very interesting. She landed on the leaf on which the nest was built about 2 cm away from the nest—something that returning foragers seldom do—they mostly alight on the nest. Having done that, Blue sat on the leaf, and Red sat on the nest, and they went through what might be called a war of attrition for over 5 minutes; Blue would attempt to get on the nest but Red would block her way and try to grab the food. Having neither succeeded in attracting the attention of the queen nor in climbing onto the nest without losing the food-load to Red, Blue 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 Blue climb onto the nest and took the food-load from her mouth but at the same time Red pounced on Blue and bit her. Before too long, Blue managed to escape from the clutches of Red 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, Red was the next most dominant individual and I had little doubt she

would be the next queen after I removed the present one. But to my surprise, it was Blue who became the next queen, in spite of Red's presence. Indeed, Red stayed on for over a month after Blue 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.

Why was Red so aggressive towards Blue compared to her behaviour towards other individuals? Why was the queen so 'considerate' towards Blue? Was there some kind of alliance between Blue and the queen? Did this in any way influence Blue's becoming the next queen when I removed the original queen, even though Red was higher in the dominance hierarchy?

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 Blue and Orange (different from the Blue and Orange of the two previous stories), both more or less equally dominant. When I removed the queen on the 9th of March 1985, for whatever reason, Blue took over the place of the queen and Orange promptly left the colony. However, Blue 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 Blue 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 Orange had not quite given up.

She would occasionally come back, as if to check on how Blue was doing. She would never spend the night on the nest but would only visit occasionally. By about the 20th of March, Orange returned for good and Blue 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, Orange to lay eggs in.

The story does not quite end there. Blue 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, Orange was doing. After a few days Blue decided to rejoin the nest but not before a great deal of hostility by the resident wasps. Blue had to spend nearly a whole day and be subordinated by several residents before she was accepted back. 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 Blue 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 Orange? Wasp politics?

So, are animals conscious of their actions?

In the preceding sections, I have left so many questions unanswered. It will probably be impossible to answer most of these questions as long as we deny animals the capacity of consciousness that we so easily permit ourselves. Based on the arguments I have presented and the complex behaviour of social insects that I have described, I leave it to the readers to decide for themselves whether animals are conscious of their

actions. But my own prejudice must be quite clear. In my opinion, nothing is gained by invoking a definition of consciousness that automatically eliminates animals. It is only by understanding animal and human behaviour along a gene culture continuum and indeed, along an animal-human continuum that we can ever hope to fully appreciate the real meaning of consciousness.

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