

Observational study of animal behaviour: From instinct to intelligence

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Ethology is the science of the study of animal behaviour. Begun as a passion and pastime of just a few individuals, ethology has grown into an elaborate scientific discipline with ever widening horizons. After a brief discussion of the history of ethology, I give a few examples of excellent ethological research which could easily have been done anywhere in India but were not! I then give a few examples of ethological research that were done in India and discuss briefly why so little ethology is done in India although it is an obvious choice for Indian biologists embarking on a research career. I argue that the study of animal intelligence provides a unique opportunity for Indian ethologists to provide international leadership. Ethologists have traditionally avoided the question of animal intelligence. The main justifications for this attitude are 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. None of these justifications are satisfactory and there is a strong case for the study of animal intelligence. I give a number of examples from my study of primitively eusocial wasps that strongly suggest complex, intelligent behaviour and speculate that cognitive abilities of the wasps and other insects may have played an important role in social evolution.

ETHOLOGY is the science of the study of animal behaviour. But, to quote Medawar and Medawar¹, it 'is not merely an alternative designation of the science of behaviour: it is a term that stands for a genuine revolution in biological thought. Ethology is rooted in the *observation* of animal behaviour, an activity that only simpletons think simple. ... observation is a difficult and sophisticated process calling upon all the intellectual virtues: attention, patience, heightened awareness, caution in coming to conclusions, courage in framing expectations'. It will be one of my endeavours to demonstrate that ethology has lived up to Medawars' expectations!

A rapid history of ethology

A definitive history of ethology has not been written although it eminently deserves to be. The following is

then my own *ad hoc* history. I think it is reasonable to recognize five phases in the development of ethology. The first may be called *pre-ethology* and happened prior to about the 1940s. During this phase animal behaviour was the passion and pastime of a few eccentric people, far from an organized academic activity. Notable players of the game during this period were: Charles Darwin², who wrote *The Expression of the Emotions in Man and Animals*; the Russian physiologist Ivan Pavlov, who discovered *classical conditioning*; the inimitable German, Jakob von Uexküll³, who used the lowly tick to show that each animal lives in its own sensory world or *Umwelt*; and Douglas Spalding⁴, a family tutor to the Bertrand Russell household, for whom it appears that the bright Russell children left enough time to do experiments on newly hatched chicks and prove that they are born with an innate ability to peck accurately at grain on the ground.

The second phase may be called *classical ethology* and lasted from about 1940 to about 1960. This period was characterized by two bitterly opposed schools of activity – the *ethologists* in Europe and the *behaviourists* in North America. Niko Tinbergen and Konrad Lorenz, being prominent amongst the ethologists, formulated the systematic observational study of animal behaviour under natural conditions^{5,6}. Behaviourists like Watson and Skinner⁷ sought to treat virtually any available animal as a black box and use it in extremely well-controlled artificial laboratory conditions with the hope eventually of understanding human behaviour. Not much came out of this hope but the experimental and statistical techniques that they and their followers developed are coming in handy as the ethologists are maturing into doing more and more experiments.

The third phase is that of *modern ethology*, which I argue lasted for just about ten years in the 1960s but had a profound influence on the future of ethology. Two activities of great significance can be traced back to this period. One is the integration of ethology and neurobiology to give rise to neuroethology in the hands of such people as Hess⁸, Hailman⁹, Griffin¹⁰ and others. The second is the shedding of the naive interpretation of natural selection as acting for *the good of the group or species* and the realization that, except under very

special circumstances, the good of the individual (selfishness) overrides the good of the group (altruism). This idea, championed by people like Williams¹¹ and formalized by Hamilton¹² was directly responsible for the subsequent growth, the present widespread practice and the glorious future expected of ethology.

The fourth and present phase is often labelled as *behavioural ecology and sociobiology*¹³⁻¹⁵. I reckon its beginning in about 1970 and predict that it will lose its identity in the process of giving rise to an extremely multidisciplinary, as yet, unnamed field of activity around the turn of the century. The central theme of the present phase of ethology is to understand every aspect of animal behaviour as an efficient adaptation engineered by natural selection. One can get a glimpse of the nature of behavioural ecology and sociobiology by glancing at its favourite topics of research: The economics of animal behaviour; Prey-predator co-evolution; When to live in groups; The battle of the sexes; Selfishness and altruism, and so on.

The fifth phase is that of the future, which will hardly be recognizable as the offspring of the previous phases. There is no doubt that it will draw together such apparently diverse fields as population biology, physiology, ecology, genetics, evolution, molecular biology, ethology, anthropology, psychology, sociology, botany, economics and political science. One only has to look at the following titles of recent research to see that this is no exaggeration. Consider, for example: Seed abortion in plants - parent-offspring conflict or sibling rivalry; The wave of advance model for the spread of agriculture; Evolution times of languages; The dynamics of a heroin addiction epidemic; Co-operation amongst nations as a prisoner's dilemma game; B-chromosome in a parasitic wasp - the most selfish DNA known!

Some fine examples of ethological research

I give below four of the many possible examples of the finest pieces of modern ethological studies. The examples are chosen not only to justify Medawar's description of ethology but to show how each one of them could so easily have been done by any biologist employed in the remotest of Indian universities.

Competition for resources

Competition for limited resources is a nearly universal fact of life for most animals. Indeed, natural selection, based as it is on the struggle for existence, is a direct consequence of such a competition. When there are habitats of differing qualities but none can be defended or monopolized, animals should be expected to adjust their distribution between habitats such that each individual enjoys the same success. This has been termed as *ideal free distribution*¹⁶. But are animals

capable of distributing themselves in this fashion? Milinski¹⁷ did a simple experiment with six fish in a tank and provided them with a certain quantity of food at side A and twice the quantity of food at side B of the tank. Within minutes there were two fish at side A and four at side B. When the quantities of food between the sides were reversed, the fish quickly adjusted themselves so that there were four fish at side A and two at side B. Clearly, the fish must have kept sampling the rate of food yield on both sides from time to time and stayed at the most profitable location at any given time.

Even when the resources can be defended, ideal free distribution may occur. Whitham¹⁸ studied a gall-making aphid in which stem mothers settle down on the leaves of the narrow-leaf cotton wood *Populus angustifolia* to make galls and reproduce parthenogenetically. More offspring are produced on larger leaves but the number of offspring decreases as more and more stem mothers make their galls on a given leaf. One should expect that settling down on a smaller leaf must sometimes be as good as settling down on a large but crowded leaf. Whitham's measurements produced the remarkable result that the average success of stem mothers at different levels of crowding was the same. This is because if the aphids wanted to be alone they had to settle for a smaller leaf and if they went for a large leaf they had to live with neighbours. In addition, however, the stem mothers arriving on a leaf engaged in sparring matches to occupy positions close to the mid rib, which has the highest amount of sap and thus leads to the largest number of offspring. What this means, of course, is that biological systems have endless richness and that the deeper one probes the more one understands.

Sex change in fishes

Many species of fish are known to change their sex midway through life. It is true that this is possible because of their labile system of sex determination, but what might be the evolutionary advantage of doing so? Even more puzzling is the fact that some species first become males and then females (*protoandry*) while others choose to start as females and then become males (*protogyny*). Should one treat this as a quirk or look for an adaptive explanation for protoandry and protogyny too? The philosophy of the ethologist is to keep looking for adaptive significance at every possible place, for assuming that something is just a quirk and not the result of natural selection amounts to giving up and ceasing to unravel the mysteries of nature.

Warner¹⁹ and others have developed a theory of the evolution of such sex change. Like most other animals, fish grow in size as they grow older. If the advantage of being large is greater for one sex than for the other, then a winning strategy would be to be of that sex when young and small for which small size is not as much of a

disadvantage and change over to that sex when old and large for which large size is particularly advantageous. In many species larger females produce more eggs than smaller ones and so it is advantageous for females to be large. In those species where there is intense male–male competition, however, small males fare so poorly compared to large males that being a small male is much worse than being a small female. The prediction then is that in those species where male–male competition is intense, one should see protogyny and in those species where male–male competition is not so intense, one should see protoandry. Indeed, this does seem to be the pattern observed in nature. Species such as the blue-headed wrasse show intense male–male competition and protogyny. On the other hand, anemonefish such as *Amphiprion* show less male–male competition and protoandry.

Nepotistic bee eaters

In many species of birds such as the Florida scrub jay, the Galapagos mocking bird, the jungle babbler, the acorn woodpecker, the pied kingfisher, the splendid wren and the white-fronted bee eater, some individuals postpone breeding and help other breeding pairs of their species in the often difficult task of rearing chicks²⁰. Typically, helpers contribute to feeding the chicks, feeding the parents and guarding the nest. The obvious question is why should helpers help? To answer this question, Emlen and Wrege sexed (by laparotomy, because the sexes cannot be identified externally), individually marked and intensively observed a large population of the white-fronted bee eater in lake Nakuru in Kenya. They found that this species, which incidentally is a close relative of our very common small green bee eater (one more reason why similar research could easily have been done in India!), lives in extended family units or clans. In each breeding season numerous clans aggregate to form large colonies of about 200 birds each. About 50% of all nests have at least one non-breeding helper. Every year Emlen and Wrege²¹ painstakingly recorded, for every nest, the number of helpers, the identity of the breeders and that of the helpers, the clutch size, hatching success and fledgling success. In addition, they were able to determine the genetic relatedness between the helpers and the helped.

With such data Emlen and Wrege²¹ tested different hypotheses for how helpers might benefit from helping. They found no evidence that an individual increases the chances of its survival by being a helper, nor did they find that helpers are more likely to become breeders in the future. Those that did become breeders were not significantly more successful than those without prior experience as helpers. However, helpers significantly increased survival of the nestlings and helped only when

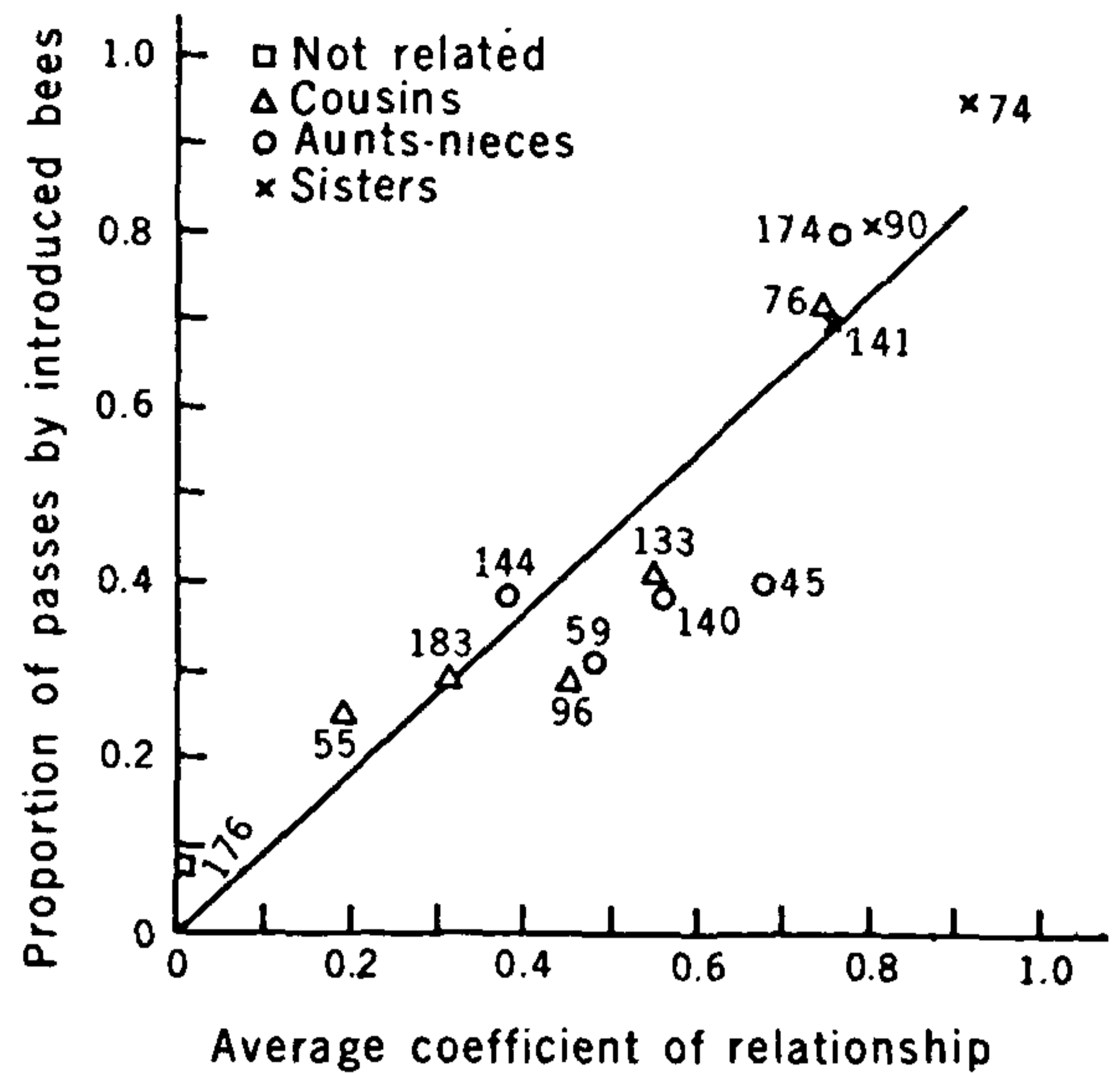


Figure 1. Individuals of the primitively eusocial bee *Lasioglossum zephyrum* were raised in the laboratory. In artificially constituted laboratory colonies guard bees were presented with intruder bees whom they had never encountered before. But these intruders were, in fact, related to the guard bees as sisters, nieces, cousins or were unrelated to them. The probability of acceptance into the nest of the intruder bee by the guard bee was significantly positively correlated with the average genetic relatedness between guard and intruder bees. After Greenberg²³ (© AAAS; reproduced with permission).

they were rather closely related to the nestlings. In other words, Emlen and Wrege found clear evidence against hypotheses based on direct benefit to helpers and strong evidence in favour of indirect benefit to helpers postulated by the inclusive fitness theory of Hamilton¹². For more details of this study, see also reference 21.

Kin recognition

Hamilton's¹² inclusive fitness theory or the theory of kin selection, as it is often called, predicts that animals should be more altruistic towards their close genetic relatives and relatively less so to non-relatives or distant relatives. An obvious question then is whether animals can distinguish their close relatives from non-relatives or distant relatives. For some 15 years after the publication of Hamilton's seminal papers, ethologists did not investigate this question: they assumed that by indirect factors such as familiarity or physical proximity, animals would automatically differentiate close from distant relatives.

In 1979 Greenberg²³ set out to investigate whether animals have a direct way of discriminating their genetic relatives from non-relatives. He used the sweat bee *Lasioglossum zephyrum* that lives in colonies of several

female bees in nests in underground tunnels. Within the nest, only one bee is the fertile queen while the others work to rear the queen's brood. The queen is usually the sister or mother of the workers. If the workers are to direct their altruistic labours to close genetic relatives only, they should ensure that no unrelated bee enters their nest. This task appears to be performed by one of the workers who takes on the role of a guard, positions herself at the entrance of the nest and inspects each incoming bee by smelling her.

Greenberg²³ used laboratory colonies and presented guards with their sisters, aunts, nieces, cousins as well as some unrelated bees and recorded the probability of each of these bees being allowed to enter the nest by the guard. With this simple experiment he obtained the remarkable result that there was a statistically significant positive correlation between the probability of acceptance of an intruder bee by the guard bee and the genetic relatedness between the guard and the intruder (Figure 1). Thus, sweat bees have ways of assessing their kinship with other members of their species. Stimulated in part by this result, ethologists have begun to investigate the kin recognition abilities of a large number of different animal species ranging from marine invertebrates to humans (for reviews see references 24–26).

Some examples of ethological research in India

Although I lament the great paucity of good ethological research carried out in India, I do not wish to leave the reader with the impression that nothing is being done here. I will, therefore, first present three examples of ethological research from India which rank among the finest pieces of ethological research done anywhere in the world and then will also give one example from my own research.

Mother mouse sets the clock of her pup

In a variety of animals and plants many features such as body temperature, rest/activity levels, hormone levels, etc., vary in a rhythmic fashion with a periodicity of 24 hours. In many cases it is known that these periodic variations are controlled by an endogenous biological clock with a periodicity of about 24 hours. The endogenous clock is reset everyday based on the day/night cycles in the environment, with the result that small differences in the period of the endogenous clock go unnoticed. By maintaining the animals or plants in continuous light or continuous darkness, however, these differences can easily be uncovered because the difference accumulates over a period of time. Thus, an endogenous rhythm is said to free-run when denied external cues and it is said to entrain when provided

with external cues. Such endogenously controlled rhythms are called *circadian rhythms*. For example, nocturnal mammals show a circadian rhythm in their rest/activity cycles such that they will be active at nights and will rest during the day. Their endogenous rhythm is normally entrained by the light/dark cycles in the environment caused by day and night. The newly born pups, however, stay in underground burrows for several days after birth. Moreover, they do not even open their eyes for many days after birth. How then do the circadian rhythms of these pups work? How does their clock reset itself? Viswanathan and Chandrashekar²⁷ tested the hypothesis that since the mother is with the pups during the day, which is her time of resting, and away from them during the night, which is her time of active foraging, the pups may use the presence/absence cycles of the mother to entrain their clocks. First they showed that pups free-run in the absence of the mother and then by introducing the mother in a cyclic fashion they demonstrated that cycles of presence and absence of mother mouse entrain the circadian clocks of pups.

Foraging trails of ants

Leptogenys processionalis is a common ant whose long and branched foraging trails are inevitable companions of those of us who are in the habit of walking or jogging in the early hours of the day in parks or in other areas of Bangalore and its surroundings. This ant preys on termites and occasionally on other arthropods. The function of the trails is to sample as wide an area as possible in search of prey. Ganeshiah and Veena²⁸ asked if the branching pattern of these foraging trails is so designed as to maximize efficiently the ratio of the area sampled to the distance travelled by the foragers. They traced the branching patterns of a number of trails and quantified them by using a method originally developed for studying the branching patterns of rivers. This method yields branching coefficients in such a way that the smaller the value of the coefficient, the more efficient is the trail system. The values obtained for *Leptogenys processionalis* ranged from 2.46 to 3.75, indicating that the trails of this ant are somewhat less efficient than the branching pattern of bronchioles in the human lung but more efficient than the branching pattern of trees or river systems. It is reasonable to expect that natural selection would have favoured those genotypes of the ant that were capable of sampling a large area with less effort. Ganeshiah and Veena went on to show that the branching process is a result of independent decisions by different ants rather than a collective decision by the whole colony and also that the branch angles are a trade-off between the cost of increased travel necessitated by small angles and resistance to the flow of ants by angles close to 90°.

How do bats locate frogs?

The Indian false vampire bat *Megaderma lyra* belongs to a group of echolocating bats that prey on larger arthropods such as moths, beetles, grasshoppers and cockroaches, and on smaller vertebrates such as frogs, geckos, lizards, fish, mice, birds and other bat species. A question of obvious interest is: How do these bats locate their prey and how are they perfectly capable of doing so even in the dark? Since these are echolocating bats, the obvious answer might be that they do so by echolocation. Marimuthu and Neuweiler²⁹ did a series of simple experiments, especially regarding how *M. lyra* locates frogs. Their first observation was that the bats detected and caught the frogs only when the latter moved. This automatically precluded dead frogs from being caught. Their next observation was that even dead frogs were located and caught if moved by the experimenter. The clinching evidence, however, came from an experiment which showed that when dead frogs were pulled over the wet surface of a glass plate to eliminate any noise, the bats were no longer successful in catching the frogs (Figure 2). Thus, even though these bats are capable of echolocation, they do not use it to catch moving prey off the ground. Additional simple experiments showed that the bats differentiated between palatable and unpalatable prey only after catching them. For example, noisily moved dead toads and dead frogs covered with toad skins were located and caught but soon discarded. These results pave the way for ecological investigations to understand why this bat does not use echolocation to locate prey on the ground.

The mechanism of nestmate discrimination in a primitively eusocial wasp

Ropalidia marginata is a primitively eusocial wasp in which new colonies are initiated by one or a group of female wasps. Female wasps eclosing on these colonies may either leave to initiate their own new colony or may stay back in their natal colonies. In all multifemale colonies only one individual is the queen and the others work to rear the queen's offspring. Because female wasps are capable of starting their own single foundress colonies and yet so many of them prefer to remain as workers in multifemale colonies, we are using this species to try and understand how such altruist behaviour evolves³⁰. A widely discussed hypothesis is that worker behaviour is favoured by natural selection because of the high genetic relatedness between workers and the brood they rear, created by the haplodiploid genetics of the hymenoptera¹². To test the validity of this explanation, we measured intracolony genetic relatedness. To our surprise we found that it was very much lower than that expected. This is because polyandry (multiple mating by the queen) and serial

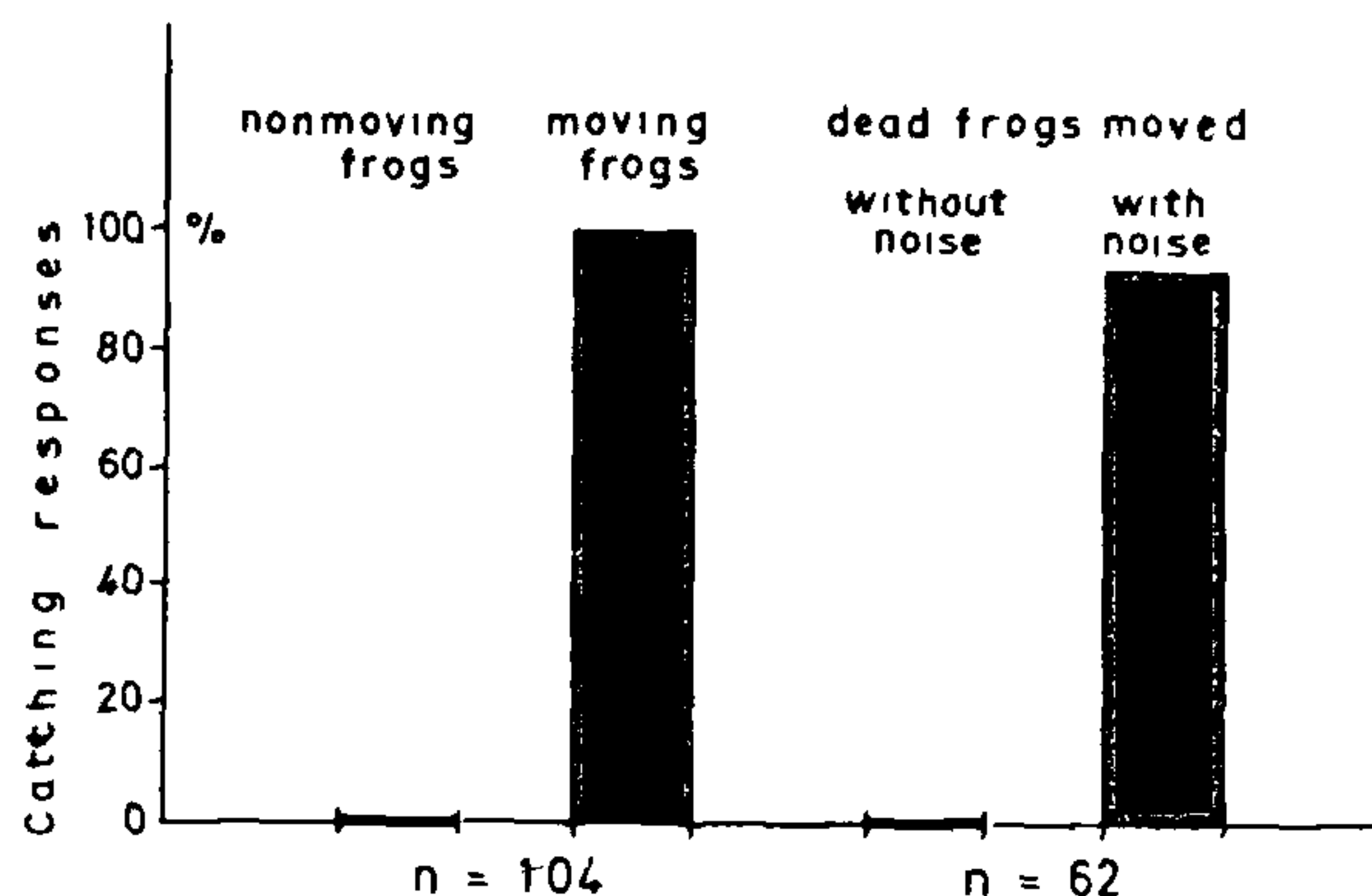


Figure 2. Percentage of catches for stationary versus moving frogs and for dead frogs moved by pulling, with and without generating noise. After Marimuthu and Neuweiler²⁹ (© *J. Comp. Physiol. A*, reproduced with permission)

polygyny (frequent replacement of the queen) result in simultaneous production of different matriline and patriline within a colony³¹⁻³⁴.

Before concluding that the haplodiploidy hypothesis for the evolution of worker behaviour is therefore not valid, we had to rule out the possibility that workers discriminate between different levels of genetic relatedness within their colony and direct their altruism preferentially towards their close genetic relatives only. To test this possibility, we undertook a study of the mechanism of nestmate discrimination in this species. Based on behavioural interactions shown by the wasps towards their nestmates and non-nestmates outside the context of their nests, we developed an assay of discrimination. Using this assay we were able to show that female wasps can discriminate between their nestmates and non-nestmates provided both the discriminating individuals and the discriminated individuals were exposed to a fragment of their natal nest and a subset of their nestmates. We concluded from these results that the labels on the bodies of the wasp used as cues in the discrimination process and the templates in their brains with which the labels must be compared are both acquired from the nest or nestmates (Table 1). This means that all the individuals in the colony will have identical or similar labels and templates, making it unlikely that the wasps will be able to discriminate between close and distant relatives within a colony and direct their altruism preferentially to close relatives. Now we concluded³⁵ that the haplodiploidy hypothesis for the evolution of worker behaviour based on workers rearing brood very closely related to them is unsatisfactory. Our conclusion that intracolony variations in genetic relatedness are not discriminated was nevertheless a speculative one. It is gratifying that subsequent more direct experiments³⁶ have since supported this conclusion.

Table 1 Nestmate discrimination in *Ropalidia marginata*

Discriminating wasps	Discriminated wasps	Discrimination
Adults on nest	Adults on nest	Yes
Exposed	Exposed	Yes
Isolated	Isolated	No
Exposed	Isolated	No
Isolated	Exposed	No

An interdisciplinary approach

Ethology is particularly amenable to an interdisciplinary approach. The techniques and ideas from a variety of disciplines such as genetics, molecular biology, mathematics, economics, computer science and so on can be readily used to obtain a much deeper understanding of ethological phenomena. I give below just two examples, one pertaining to molecular biology and the other to neural networks.

Mating systems in birds

Birds exhibit a variety of mating systems, including monogamy, polygyny, polyandry and promiscuousness. Monogamy seems to be more common among birds than among mammals. This is usually attributed to the difficulty of rearing chicks by the mother alone. In recent years many sporadic chance observations have begun to suggest that species which are commonly thought to be monogamous are not always so. If this is true then not all the chicks for whom the father works will be his own. Whether the female partner is completely monogamous and does not mate even occasionally outside the pair bond is very difficult to prove by behavioural observations alone. Molecular biologists have developed the powerful technique of DNA fingerprinting, which is now widely used for determining paternity, when in doubt, in humans. Burke and Bruford³⁷ applied DNA fingerprinting, using probes developed for humans, to wild populations of the house sparrow and illustrated how it could be said with a great degree of certainty that at least one of the chicks in a nest was not the biological offspring of the presumed father. This technique is now being increasingly used to confirm behavioural observations regarding parentage and genetic relatedness.

Why do peacocks have long tails?

The peacock is a prime example of how males in many species of birds and some mammals have evolved

exaggerated and showy characters. These characters are said to evolve through the process of sexual selection because of the preference for such characters among the females of the species. Males with such characters may actually suffer a disadvantage in terms of escaping from predators, with the result that they become handicapped³⁸. Fisher³⁹ argued that reduced survival due to this handicap can be more than offset by increased opportunities to mate and thus these characters may get exaggerated by a process of runaway selection. An unanswered question in this argument is why females should prefer males with exaggerated characters in the first place. In other words, what is the basis of the aesthetic sense of the females?

In what might turn out to be a landmark study, Enquist and Arak⁴⁰ used a neural network model to show how female preferences for exaggerated male characters may develop. The starting point is selection on the ability of females to distinguish conspecific males from heterospecific males based on small differences in their tail length. A simple neural network was trained to make such discrimination and a selection was applied for accurate discrimination. The process of this training and selection, produced biases in the preference for some unexpected characters, including extraordinarily long tail lengths. Computer simulation of the co-evolution of female preference and male tail lengths demonstrated that exaggeration of tail length can occur even if it decreases the survival of the males. This approach is likely to have applications in the study of a wide range of behavioural phenomena.

Complex and intelligent behaviour

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 processes⁴¹⁻⁴³. His books provide a fascinating commentary on 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 on how most ethologists seem to have a closed mind on the question of animal intelligence.

I would like to submit that this should be a special area of focus for Indian ethologists because I think that we have a unique opportunity of taking the lead. 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.

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 realizing that, since the burrow had been inspected so many times in the recent past, the cricket may now be directly taken into it or that, since it is 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.

Another familiar objection to the possibility of intelligent behaviour especially 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 realized that it is not the size of the brain or the number of neurons but the quality and the quantity of neural connections that really matter. The small size of insect brain should, therefore, not deter us from investigating possible examples of intelligent behaviour among insects.

Almost all ethologists will admit that man was subject to 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.

An appropriate principle that should guide us while considering the question of animal intelligence is that natural selection will opt for stereotyped, instinctive behaviour if that serves best the interests of the animal in that context. Since Henry Fabre 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 digger 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.

Another important fact that needs to be emphasized is that we might expect a continuum between highly rigid, hard-wired, instinctive behaviour and flexible, intelligent behaviour within the same organism, depending upon 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 in hunting and courtship.

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 hypothesis should be whether 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 minimize 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 intelligence.

But an even better way to counter this criticism is to document carefully examples of what appear to be complex, versatile, intelligent, thoughtful, conscious, flexible and un-instinctive behaviours on the part of animals. Griffin⁴³ provides an impressive catalogue of these examples and I will not repeat any of them here. Instead, I will briefly describe some of my own observations on *Ropalidia marginata* and *R. 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 own interpretation. Nevertheless, they open up many questions and clearly point to the flexibility and complexity of the behaviour of the wasps.

A case of 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 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 end 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 thus I had no doubt that they were my wasps. What amazed me more was that the 5 wasps were not just sitting there; they had made a small nest of their own.

It then dawned on 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 of my wasps turned into great excitement. Clearly, half the population had left their declining colony and ventured on their own. Perhaps the aggressive OTBAA 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 being unable to dislodge the original queen BLATA and mend matters, OTBAA was forced to leave.

But what would be the consequence of this for those who left the colony – *rebels* and for those who stayed back in the original colony – the *loyalists*. 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 loyalists⁴⁴. 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, therefore, reasonable to conclude that high rates of aggression reduced the efficiency of brood rearing before colony fission, and the low rates of aggression in both the colonies after fission allowed efficient brood rearing⁴⁴.

The results of an examination of the caste and age composition of the loyalists and rebels before the event of fission were equally interesting. By multivariate statistical analysis of time–activity budgets, we have previously demonstrated that both in *R. marginata* and *R. cyathiformis* adult female wasps can be classified into three behavioural castes or groups, which we have termed as *sitters*, *fighters* and *foragers*^{45–47}. While there is little, if any, qualitative difference between different female wasps in a colony, there is clear-cut quantitative differentiation: the sitters spend more time sitting and grooming themselves than the fighters and foragers; the

fighters show higher rates of dominance behaviour than sitters and foragers; and the 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 colony fission, the original queen BLATA (herself a fighter), who was 72-days old on the day of 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, herself also a fighter in the colony before fission, although only 19-days old on the day of 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 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 fission (Table 2). I imagine that no sitter went with the rebels because there was only one sitter of any reasonable age, namely, BLTDA⁴⁴.

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 at least to begin to do so, we measured behavioural co-ordination within and between groups by computing Yule's association coefficients between pairs of wasps⁴⁴. We then asked the question whether there was more co-ordination 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 fission, with the loyalists and rebels behaving as two co-ordinated groups and avoiding each other⁴⁴. 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 another nest of *R. cyathiformis* under observation for the purpose of removing the queen to see who the next queen would be; 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 trying not only to avoid RT but also 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.

Table 2. Caste and age composition of loyalists and rebels

Animal	Loyalist/ rebel	Behavioural caste***	Age in days at the time of fission
BLATA*	Loyalist	Fighter	72
STNBA	Loyalist	Forager	58
OTYA	Loyalist	Forager	24
BLTDA	Loyalist	Sitter	10
BATRA	Loyalist	Sitter	5
BATYA	Loyalist	Sitter	3
STDGA	Rebel	Forager	58
RTDGA	Rebel	Forager	37
OTBAA**	Rebel	Fighter	19
OTLBA	Rebel	Forager	17
BATSA	Rebel	Forager	8

*Queen in the original colony as well as in the loyalist group

**Queen after fission, in the rebel group.

***The same caste was maintained after fission, for all animals

DBA'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, with DBA sitting on the leaf and RT sitting on the nest, they 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 on to 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 on to the nest and took the food load from her mouth but at the same time RT pounced on DBA and bit her. 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 that 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. Even sitters do a fair amount of intranidal work⁴⁷ 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.

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 wasps.

Do workers choose their queens?

During a similar queen removal experiment with *R. cyathiformis*, I once had a situation where 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 the 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 (Figures 3 and 4). 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 co-operate with DBT when she first took over as the queen? If she was simply not good enough to be a queen, why did she

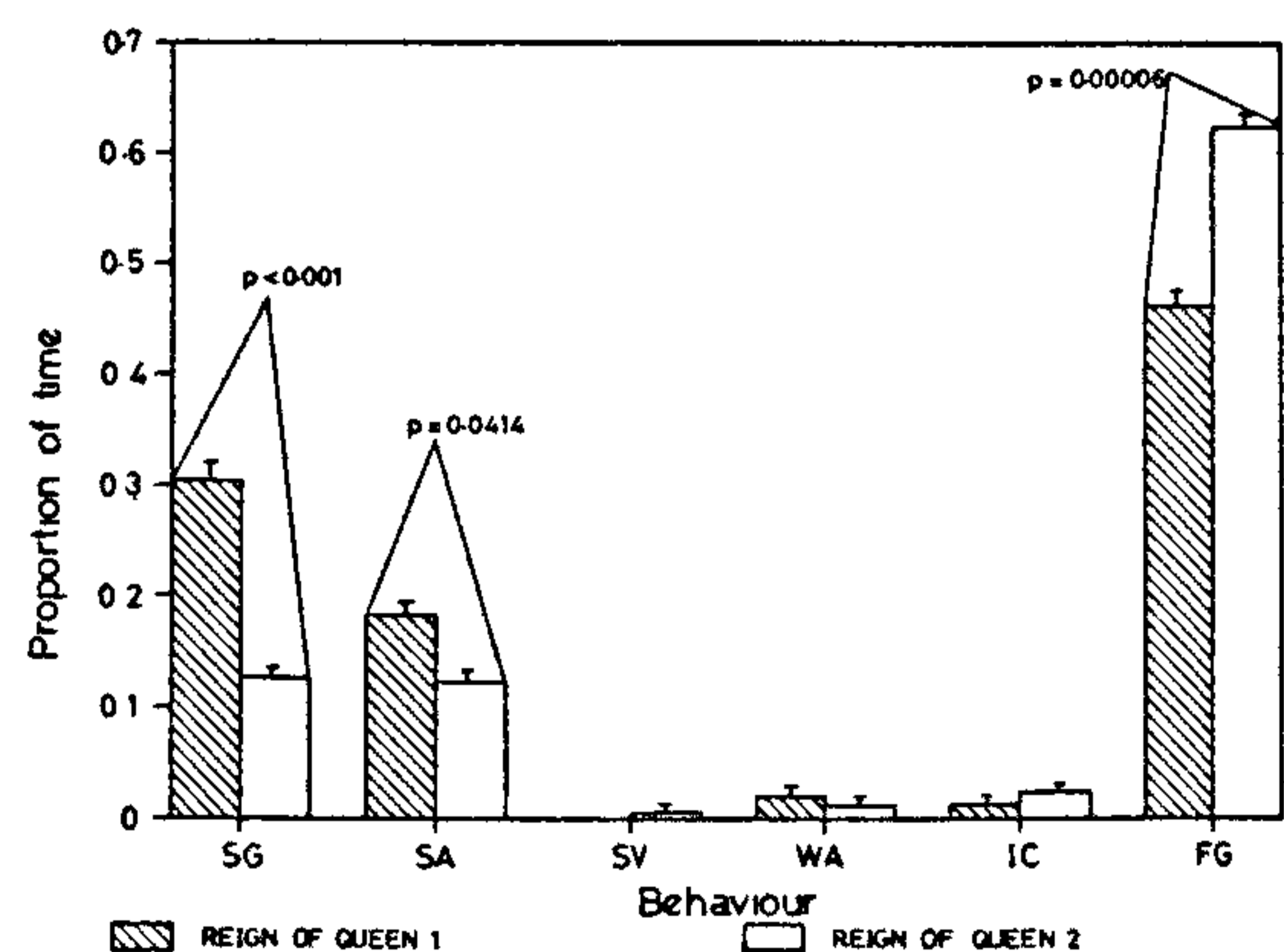


Figure 3. Behavioural variation in a group of *R. marginata* females during the reigns of two different queens. Proportions of time spent in six common behaviours by an average wasp in the colony are shown. See text for details. Statistical tests by Mann-Whitney *U* test.

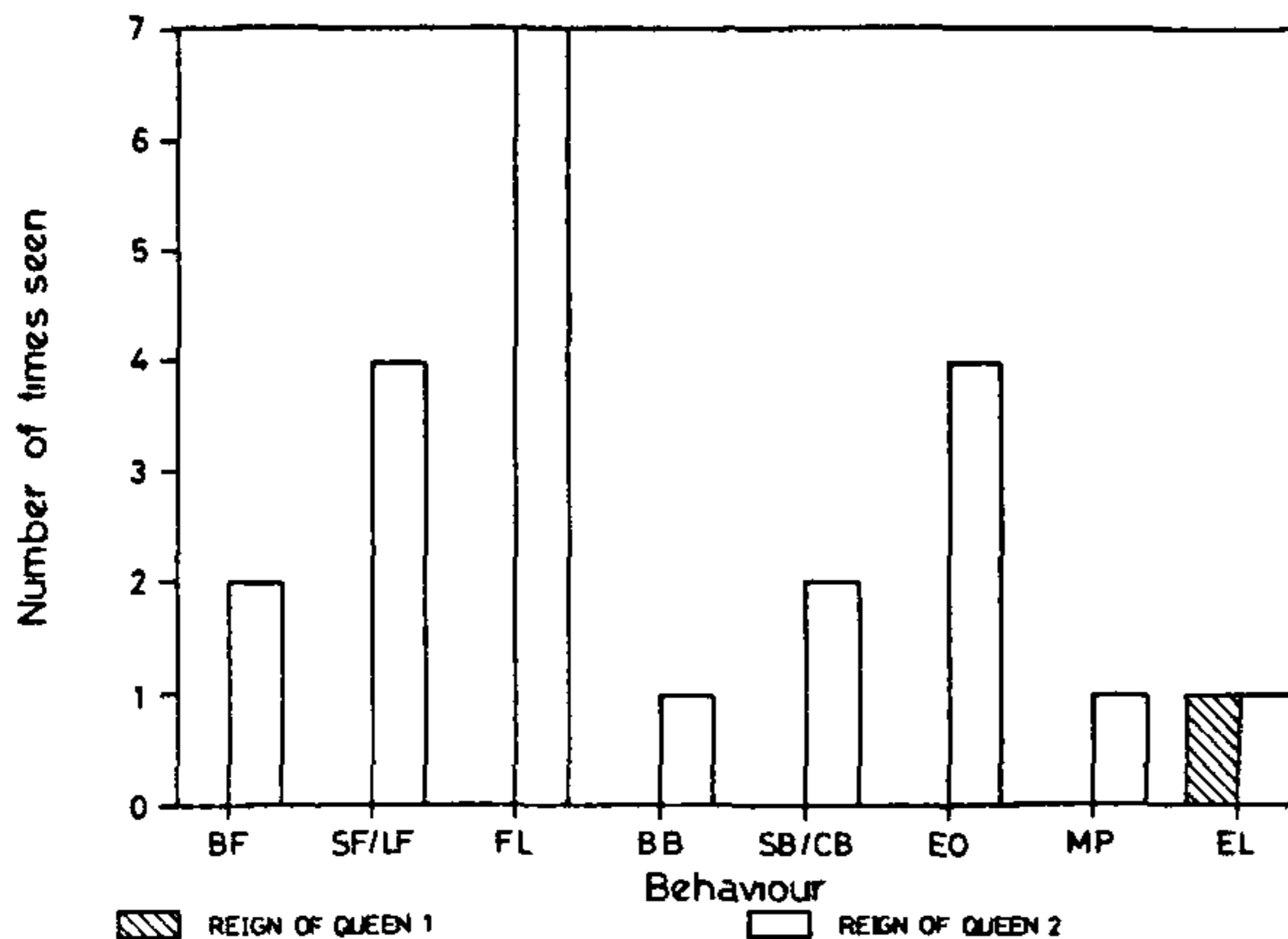


Figure 4. Behavioural variation in a group of *R. marginata* females during the reigns of two different females. The number of times each of eight behaviours were seen in the colony are shown. See text for details.

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, neither the opportunity to raise brood with particularly high genetic relatedness to themselves nor parental manipulation explains satisfactorily why workers in *R. marginata* work, but 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 choose 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 interactions, 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.

The pains and pleasures of doing research in ethology in India

Any consideration of the prospects for ethological research in India has to face a serious set of contradictions. On the one hand, it appears obvious that ethology is just the right choice for young biologists embarking on a research career in India. The most important reason for this is the easy access we have to an incredibly rich fauna and flora which can be used as model systems. Perhaps, equally important is the fact that ethological research seldom requires very expensive and/or imported equipment or chemicals. As we have seen above, the boundaries of traditional ethology are being rapidly expanded so as to include many other related disciplines. Clearly, ethology in this broad sense is likely to flourish and be one of the main activities of biologists in the foreseeable future. For all these reasons ethology provides realistic opportunities for Indian biologists to provide international leadership.

At the same time, woefully little ethological research is actually carried out in India and in some ways it is very difficult to do so in India. I would argue that the single most important reason for this is that zoology and to some extent botany are taught in Indian schools and universities as sciences of dead animals and plants. So much attention is paid to morphology and anatomy that there is no time for students to cope with the realities of the living world of animals and plants. Another factor, also a very important one, is that little attention is paid in our curricula to local faunal and floral biodiversity. For instance, it has been my experience that students who obtain an MSc in zoology from most Indian universities are usually incapable of identifying even a dozen common birds or insects in their surroundings. If they do know of some examples, these will usually be textbook examples from the western hemisphere. Yet another factor is that our education system still seems to believe in the dichotomy between mathematics and biology. It is no exaggeration to say that those students who are comfortable with elementary mathematics are advised to go on to study physics and chemistry, while those who are uncomfortable with even the most elementary mathematical concepts are advised to major

in biology. It is high time that mathematics be considered as a tool with applications in all branches of science and made compulsory for all science students at least up to and including the B Sc level.

It is sometimes said that the onslaught of molecular biology takes away the best biology students. This is paradoxical because, if molecular biologists, with all the difficulty of doing internationally competitive research in molecular biology under Indian conditions of technology and economy, can entice students to their field, ethologists, with the advantages they have for doing internationally competitive research, should be even more successful in enticing students. If the onslaught of molecular biology is indeed taking away our best biology students then, surely, the ethologists are to be blamed! It must be said, however, that a large number of our molecular biologists struggle with laboratory problems of limited interest, borrowed from western labs, and if they can be persuaded to collaborate with local ethologists to tackle problems relevant to our fauna and flora, the result would be most gratifying.

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