class of electrical impulses from the brain that are not direct responses to external stimuli but that apparently are affected by internal processes in the brain and hence appropriately called event-related potentials, EPR for short. There appears to be evidence that P300, an EPR that lasts for 300 milliseconds, may be correlated with thought processes in humans. The fact that P300s are seen in monkeys and other animals opens up the possibility of detecting thought processes in animals too, and efforts in this direction have already begun. Finally, and perhaps most important, Griffin argues that communicative behavior in animals provides an especially useful window on animal minds. We can only use this window effectively, however, if we stop thinking of animal communication signals as what Griffin calls "groans of pain" and start thinking of them as an attempt on the part of animals to assess other animals' moods and thoughts and predict their probable behavioral responses. The Dutch zoologist Frans de Waal has described some incredible instances of chimpanzee intelligence in his provocatively titled book *Chimpanzee Politics.* I will describe some of these in the next chapter and take courage from de Waal and describe some of my own observations on insects under what you will agree is an even more provocative title, "Wasp Politics."

9

The Fine Balance between Cooperation and Conflict

Domestic Conflicts in a Bird Family

Birds exhibit, more than any other group of higher animals, such "noble virtues" as monogamy, pair bonding for life, male parental care, and cooperative efforts by both parents in nest building and care of the chicks. Not surprisingly, these virtues of the birds are often extolled by poets and philosophers, especially when they are admonishing fellow humans. As we probe deeper into the secrets of bird family life, however, we find many unexpected domestic conflicts coming to the fore. A particularly startling revelation has come from the recent use of DNA technology to determine the parentage of chicks being reared in the nests of monogamously paired parents, much like the work of forensic laboratories in resolving cases of disputed parentage among humans. Many species that were fondly thought to be monogamous have turned out to be rather promiscuous. Females from apparently monogamous pairs often mate, on the sly as it were, with males from neighboring monogamous pairs and lay at least some eggs that are not sired by the partners who help them in parental duties.

A novel and more complicated domestic conflict has recently been documented by Norwegian scientists. T. Slagsvold, T. Amundsen, and S. Dale conducted a four-year study of the breeding biology of the blue tit, a small passerine bird, not unlike the common house sparrow. These birds are monogamous and both parents share in parental duties. The female lays about 10 eggs in a span of about 10 days and incubates them. The male does not help with the incubation, but he feeds the female while she incubates, and later, when the chicks hatch, both parents feed them. When should the female start incubating? If she starts too early (say, as soon as she lays her first egg), the chicks will hatch on different days and the parents will have a very asynchronous brood to take care of. If she starts late (say, after she has already laid all her eggs), the chicks will all hatch at almost the same time and the parents will have a very synchronous brood.

It turns out that synchronous and asynchronous broods have very different consequences for the male and female parents. This was discovered by artificially manipulating broods to produce especially synchronous or asynchronous broods. Males had a higher chance of surviving to breed again the following year if they cared for an asynchronous brood than if they cared for a synchronous brood. Conversely, females had a higher chance of surviving to breed the following year when they cared for synchronous brood rather than an asynchronous brood. Thus the mother is better off raising a synchronous batch of brood while the father is better off with an asynchronous batch of brood. The most likely reasons for these male-female differences are as follows. Males, while participating in parental care, are apparently not as conscientious as the females. They take care of the larger and stronger chicks and when these chicks are successfully fledged, they stop caring for chicks and concentrate on territorial defense and molting to enhance their future survival probabilities. The burden of difficult and prolonged care of late-developing, small, and weak chicks falls on the mother. When the chicks are all of more or less the same age, the mother thus has more help from the father, who in turn has to work harder because all the chicks satisfy his criteria of being big and strong. When the brood is asynchronous, however, the male benefits by stopping his work early while the female carries on alone, caring for the smaller and weaker chicks and in the process lowering her chances of being alive and fit to breed again the following year.

Now why should males and females be so different in their commitment to parental care? First, female parental care is more fundamental, and as soon as there is any opportunity for one of the parents to desert, it is usually the male who is the first one to seize it. This happens throughout the animal kingdom, and may be related to the fact that females invest more in their offspring, starting right from the substantial cost of an egg, while males invest much less, often nothing more than inexpensive sperm. Hence females have much more at stake in the survival of their offspring than males do. Second, the small, late-hatching chicks in a nest are more likely to be sired by neighboring males in extra-pair copulations, so that the resident male has even less interest in the welfare of these particular chicks. Thus one would expect a conflict between the two parents on the question of whether the brood should hatch synchronously or asynchronously. But this conflict remains hidden because only the female incubates, and thus only she can decide how synchronous the brood should be. In addition to the many examples of overt conflict seen throughout this book, there may be other such hidden conflicts that can be uncovered only by careful experimentation.

Until not too long ago, unexpected conflicts among animals were dismissed as being pathological. The evolutionary approach to animal behavior permits us to face such unexpected conflicts head on and even to predict when conflicts may occur and how they may be resolved. As a bonus, our understanding of animal behavior grows in richness. But if these revelations of domestic conflict in birds appear to make them unsuitable as models of good behavior, we must reflect on the fact that they are still able to maintain an external appearance of faithfully bonded monogamous pairs in spite of such hidden conflict.

Queen-Worker Conflict in Ants

We might argue that birds are not so socially evolved as some other species and hence they still experience a lot of conflict. What about the socially advanced ant societies, where the queen appears to be in complete control of the workers and the workers appear to have lost all options of revolting against the queen's authority? Is there still some conflict? It is true that many species of ants and bees have reached that pinnacle of social evolution where workers are locked into sociality and can neither lead a solitary life nor mate and reproduce—two prerequisites for revolting against the queen's authority. And yet if we look deeper, we see conflict here also. Even when workers cannot drive away the queen and take her role or leave the colony to start their own, natural selection would be expected to favor workers who get as much benefit as possible from the queen. Of course natural selection is impartial, so it would simultaneously act on queens to yield as little benefit as possible to the worker. Thus the conflict between queen and worker would come to the fore.

Consider an ant colony, where the workers are the queen's daughters. Because workers in the Hymenoptera are more closely related to their sisters than they would be to their own offspring, workers would be expected to cooperate with their queens in rearing the queen's female brood. Recall that workers are related to their brothers (the queen's male brood) by only 0.25. Thus workers should be more reluctant to rear their brothers and should prefer to rear their own sons. Rearing a combination of sisters and sons would be their ideal choice. The worker's sons are the queen's grandsons and are thus less related to her than her own sons would be. A queen would therefore prefer that workers rear her sons and daughters. Here is a region of conflict between queens and workers. This conflict can become intense because in many species of social Hymenoptera workers have not entirely lost their ovaries; they often have at least small ovaries and can lay a few unfertilized eggs, destined to be males. Queen-worker conflict over male production is now well known in many ant species. The workers attempt to lay haploid eggs and the queen attempts to eat them and then replace them with her own haploid eggs.

If the workers fail to win in this conflict by laying enough haploid eggs, all is not lost. It turns out that there is yet another weapon in their arsenal. After all, it is the workers who feed all the larvae and surely they can feed their sisters more than their brothers. In fact, considering that the workers are related to their sisters by 0.75 and to their brothers by 0.25, we should expect them to give three times as much food to their sisters as they would to their brothers. Shocking as it may seem, workers in many (but not all) ant colonies seem to do exactly this, although they may be somewhat imprecise in apportioning food in the ratio of 3 to 1. This is a rather striking confirmation of the theoretical expectation. But as they say, exceptions prove the rule. So we must find an exception to the rule that workers should feed their sisters three times as much as they feed their brothers and see if that exception is also found in nature.

Robert Trivers and Hope Hare, who originally made the bold suggestion that workers should bias their investment in the ratio of 3 to 1, have postulated two exceptions. In some ant species, several queens simultaneously lay eggs in each colony; these are called polygynous colonies.

Here the workers care for larvae that are not always their sisters because they may be the daughters of other queens in the same colony. The workers' relatedness to these larvae may be very low and would depend on the genetic relatedness between their mother and the mother of the larva concerned. Even if the mother of the larva was the sister of the worker's mother, the larva would be her cousin, and cousins are less closely related than sisters. So workers would not be selected to invest in female and male brood of the queens in the ratio of 3 to 1. In the few polygynous colonies studied from this point of view, the ratio of investment is not even approximately 3 to 1. Prediction confirmed once again.

The second exception that Trivers and Hare came up with is even more interesting. Some species of ants have abandoned the habit of producing a large number of sterile workers before producing future queens and males, since this is quite a costly undertaking. Instead they produce just enough workers to raid neighboring colonies of related species of ants and forcibly bring back worker pupae from the raided nest. These are called slave-making ants and the species providing the slaves (pupae), although none provides willingly, are called the slave species. When pupae of the slave species mature in their foster colonies, they wake up and start working; they don't seem to know that they have been kidnapped. But imagine what would happen if a mutation arose in the slave species that did not program them to invest in female and male larvae in the ratio of 3 to 1. Such a mutation does not suffer any great disadvantage compared with the wild type, because the ant slaves work for different species altogether and will yield them no fitness anyway. So natural selection should not be expected to have perfected the adaptation of the 3 to 1 investment ratio in slave species as effectively as it might have done in the nonslave species. This indeed appears to be the case.

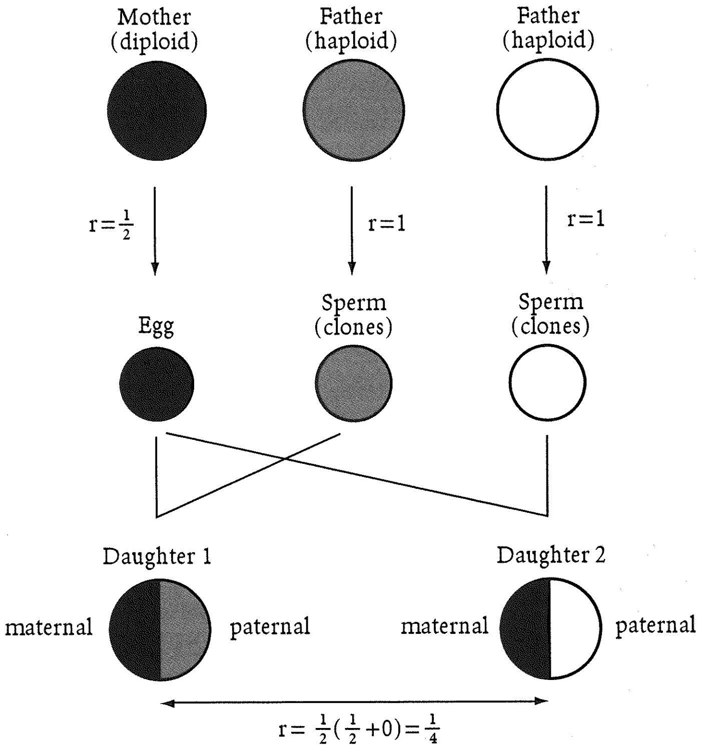
If only for the sake of amusement, we can wonder who wins in each case of conflict. In normal monogynous colonies, the workers seem to

have the last laugh because they are in charge of feeding and they can bias investment in male and female larvae in the ratio advantageous to them and not in the ratio advantageous to the queens. In polygynous colonies workers are forced to care for the brood of several queens and therefore cannot have their way; hence the queens benefit from their predicament. In slave-making species, queens benefit from the fact that the workers are aliens and have no interest in upstaging the queens. But the conflict is always there and it is often resolved in unexpected ways.

Worker-Worker Conflict in Honey Bees

Francis Ratnieks has come up with another twist to the story of conflict within the apparently harmonious colonies of advanced insect societies. Recall that if the mother queen mates with just a single male, the workers will all be full sisters and thus related to each other by 0.75 and to their brothers by 0.25. In such a situation, workers should prefer their own sons over their brothers. Ratnieks has argued that any worker should also prefer any other worker's sons (her nephews) over her brothers, because a worker is related to her nephews by half the value of her relatedness to her sisters and that comes to 0.375 when sisters are related by 0.75. Thus workers should have a common interest in revolting against the mother queen and laying their own male-destined eggs. The workers should not have much conflict among themselves because they would rather rear male eggs laid by each other than those laid by the queen.

But if the queen mates with several males and produces daughters by using sperm from different males, the workers will now quite often be stepsisters or half sisters, related to each other by only 0.25. Although each worker should continue to prefer to rear her own sons rather than her brothers, workers should now cease to prefer each other's sons. The son of a half sister would be related by only half of 0.25, which is 0.125. Each worker should now prefer the queen's sons over another worker's sons. Although their first preference would still be their own sons, they would not agree on which of them should produce the male eggs. Indeed, Ratnieks has argued that workers should police each other and



Genetic relatedness under haplodiploidy with multiple mating. Notice that the genetic relatedness between half sisters is 0.25.

destroy any eggs laid by each other because they would no longer (owing to multiple mating by the queen) prefer nephews over brothers.

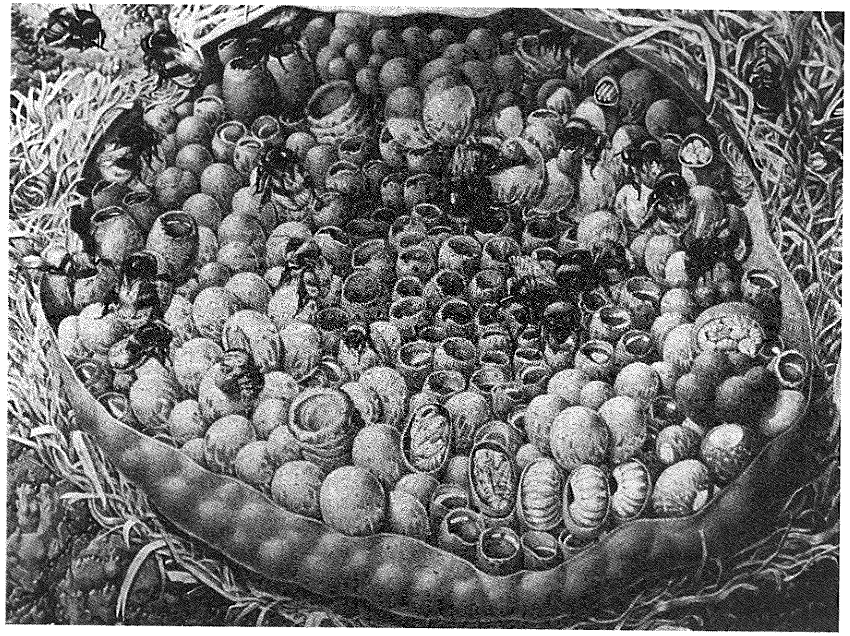
The honey bee society is a good system to use to test this prediction since the queens are known to mate with 10 to 20 different males. Ratnieks collaborated with Kirk Visscher, the man whose reluctance to convict *Apis mellifera* of nepotism we saw earlier. Ratnieks and Visscher used the European honey bee *Apis mellifera* and asked if workers actually police each other by eating each other's eggs, as predicted by the theory. They found that while only 0.7 percent of the worker-laid eggs survived after 24 hours, 45.2 percent of queen-laid eggs did so after the same time period. It seems rather ironic that the queen ultimately benefits from the inability of the workers to agree on which one of them should lay the male eggs, although they all agree that it is not the queen but they who should be doing so. Is the queen's habit of mating with several males a strategy to disrupt the workers' unity and get them to fight with each other?

Disease As an Enhancer of Social Conflict

Parasites that cause diseases of varying intensities are ubiquitous in the natural world. But the role of disease in shaping the ecology and evolution of their hosts has only recently begun to be properly appreciated. Parasite load has, for example, been shown to be an important parameter that females use to assess the quality of their mates. In response, males are known to evolve elaborate secondary sexual characters to impress upon females their health in general and their ability to resist parasites in particular. Recently, an even more profound role that parasites play in modulating social evolution has come to light.

As we saw with the honey bees, queens in many social Hymenoptera mate with several males and simultaneously use sperm from different males to produce several patrilines of daughters. Daughters belonging to different patrilines would of course be half sisters, with a coefficient of genetic relatedness of 0.25. The fitness gained by rearing half sisters would obviously be considerably less than that gained by rearing offspring. In species such as the honey bee, where workers do not have the option of either leaving or of driving away the queen and taking over her role, the habit of multiple mating may, as we just saw, set the workers against each other and help the queen. But in species where the workers can revolt, this habit of multiple mating by the queens should decrease the propensity of the queen's daughters to remain in her nest and help her raise more daughters. The question therefore is: Why should queens mate with more than one male? Would they not be better off mating with a single male and thus ensuring the cooperation of their daughters? In search of a solution to this apparent paradox researchers have begun to focus on the possible advantages of genetic variability (provided by the presence of multiple patrilines) within a colony. For instance, to the extent that task performance in the colony has a genetic basis (and we saw evidence of this in Chapter 3), genetic variability provides for a more efficient division of labor. A somewhat different kind of argument is that intra-colony genetic variability could provide effective resistance to diseases, which might otherwise spread rapidly when all workers in a colony are highly related to each other and thus susceptible to the same parasites.

Jacqui Shykoff and Paul Schmid-Hempel studied the European bumble bee *Bombus terrestris* and its intestinal trypanosome parasite, *Crithidia bombi,* and confirmed such an advantage of intra-colony genetic variability. *C. bombi* spreads from one bumble bee to another through the ingestion by bumble bees of live parasite cells during direct physical contact or through contact with the feces of infected individuals. *B. terrestris,* living in a temperate environment, suspends



Drawing of a bumble bee nest showing brood in different stages of development, wax pots filled with honey, and adults. *(Drawing by Margrit Pirker.)*

colonial life during the winter, when new queens hibernate while old queens and all workers die. In the following spring, queens emerge from their hibernation and initiate new colonies. The queens first produce daughters who become workers and later, with the help of this labor force, they produce daughters who mate, hibernate, and become queens in the next year. The parasite depends for its continued survival through the years on infecting new queens before they begin to hibernate. Infected queens are likely to pass the infection on to their daughter workers as well as their daughter queens because of the possibility of becoming infected through physical contact or contact with feces within their colonies. Laboratory experiments show that the spread of infection from one bumble bee to another depends significantly on the genetic relatedness between the source and the recipient of infection. This suggests a genetic basis for susceptibility and supports the idea that infection would spread more rapidly in a relatively genetically homogeneous colony than in a colony of genetically more variable individuals. Given a reasonable chance of their being infected, queens who mate multiply and produce genetically variable daughters should therefore be at an advantage compared with queens who mate singly and produce genetically similar daughters. Disease is thus a potential factor that selects for multiple mating by the queen, although *B. terrestris* queens seem to mate singly, perhaps for the reason mentioned below.

The *Bombus-Crithidia* story has other fascinating ramifications. In normal uninfected colonies, workers at first have poorly developed ovaries and spend all their time working for the colony to rear the queen's (their mother's) brood. Over time, however, the workers gradually develop their ovaries, and toward the end of the colony cycle they virtually revolt against queen control and begin to lay their own eggs. The success of queens therefore depends upon producing new daughter queens before workers begin to revolt. A queen that dies after producing only workers and no daughter queens gains little, if any, fitness. Curiously, queens seem to benefit from the infected status of their daughter workers. Infection retards the ovarian development of workers and thus keeps them working for longer periods of time and postpones the time of their revolt. In these circumstances queens have more time to complete the production of their new daughter queens. In principle this should provide an opposing selective force. Since queens benefit from having infected workers and such infection spreads more effectively in genetically similar lines of workers, a queen would be better off mating singly and producing daughters who are all full sisters. Disease could thus in principle select for single mating, instead of multiple mating, and this may perhaps be the reason why the queens seem to mate singly.

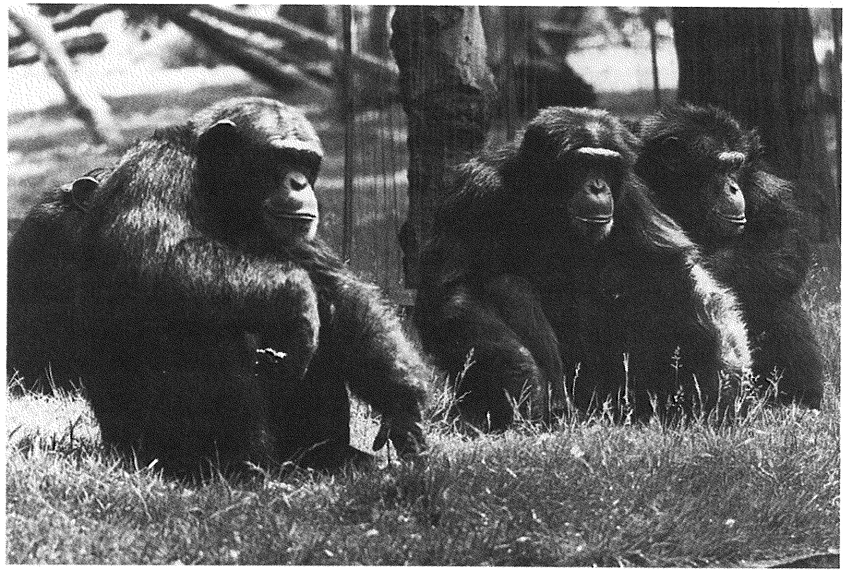
But there is a problem here. If workers in a colony are infected, the new daughter queen is likely to be infected too. A parasite that has detrimental effects on workers has similar effects on the queens. Infected queens can start new nests, but they lay eggs at a somewhat lower rate than do uninfected queens. This has been shown to lead to significantly smaller worker populations in infected laboratory colonies. So the queens should prefer to avoid infection in their colonies and should mate with many males. Obviously we do not know which factor is more important and we therefore cannot say confidently why the queens mate singly. My only purpose here is to point out the various ways in which disease can influence phenomena like multiple mating, which in turn influence levels of intra-colony genetic relatedness. All this reasoning is from the queen's point of view, because selection for multiple versus single mating is expected to act on the queen—the daughter workers have little say in this matter.

But multiple mating is only one way of increasing genetic variability in the colony. The presence of multiple queens is another way. Here it is entirely possible that workers have some say in the matter. In some ants for example, it is well known that workers decide not only how many queens may be reproductively active in their colony but even which individuals may become reproductively active queens. Now what will the workers prefer—low genetic variability or high genetic variability? Disease can have profound and unexpected consequences for the balance between cooperation and conflict, but it remains a poorly studied aspect of social life in animals.

Chimpanzee Politics

In the 1960s, Jane Goodall went to Africa to undertake her path-breaking study of chimpanzees in the wild. In the 1970s, Allen and Beatrice Gardner worked with chimpanzees in captivity and taught them American sign language. In the 1970s and 1980s, Frans de Waal spent many years watching chimpanzees in a large outdoor enclosure in the Arnheim Zoo in the Netherlands. In many ways, de Waal's research, though conducted on animals in captivity, gives us a superb picture of chimpanzee behavior, because de Waal could avoid the difficulties of observation in the wild and yet continually watch chimpanzees whose enclosure was large enough to permit them to behave naturally. De Waal's most telling observations about these animals, recorded in *Chimpanzee Politics*, concern the love-hate relationships between three males, Yeroen, Luit, and Nickie. In the beginning, Yeroen was the dominant, or alpha, male. Luit and Nickie as well as all the females treated him with respect. Luit gradually challenged Yeroen by enlisting the cooperation of the females as well as of young Nickie. The very fact that Nickie was used by Luit to wrest power from Yeroen appears to have given Nickie an advantage. It was not long before Nickie, with help from none other than the ousted Yeroen, challenged and replaced Luit as the new alpha male. Not only did de Waal witness the swinging back and forth between cooperation and conflict between Yeroen, Luit, and Nickie, but on almost every day he witnessed conflict and reconciliation among the members of the group.

In his foreword to *Chimpanzee Politics*, Desmond Morris writes of the chimps: "Their life is full of takeovers, dominance networks, power struggles, alliances, divide-and-rule strategies, coalitions, arbitration, collective leadership, privileges and bargaining. There is hardly anything that occurs in the corridors of power of the human world that cannot



The three famous chimps Yeroen, Luit, and Nikkie (left to right). *(Reprinted with permission from F. de Waal, Chimpanzee Politics: Power and Sex among Apes, 1989).*

be found in embryo in the social life of a chimpanzee colony." Not surprisingly, de Waal contends that "the roots of politics are older than humanity." Morris suggests that this message "will upset many including some of our leading political figures." If that is so, I shudder to think of what my next section will do.

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 and the number of brood being reared. I feared that, as often happens, the colony might be abandoned, bringing a premature end to my long-term study. Instead, what actually happened was far more interesting. On the evening of May 31, 1982, I had left the colony with 11 adult females, all individually marked with spots of different-colored paint. On my arrival on the morning of June 1, I noticed with dismay that only 6 of the 11 females remained on the nest. It is not unusual for 1 or 2 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. 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 5 of the missing wasps, which I could identify with certainty by their paint spots. 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 on the new nest. My disappointment at the loss of half my wasps turned into great excitement. Clearly, half the population had deserted their declining colony and ventured out on their own. Perhaps the aggressive 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 decided to leave.

But what would be the consequence of this for the Rebels that left and indeed for the Loyalists that remained in the original colony? This was easy to determine. 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 there 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 behavior 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 behavioral data on these individuals in my computer files and compare the behavior 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 toward the Rebels than the Rebels did toward them. 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 therefore that high rates of aggression reflect a high degree of conflict and that this reduced the efficiency of brood rearing before colony fission. Conversely, the low rates of aggression in both colonies after fission reflect a high degree of cooperation and this 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 31 or had revolt been brewing for some time? Was there some form of groupism even before the fission? To investigate these questions my colleagues and I measured behavioral coordination within and between subgroups (Rebels and Loyalists) using a mathematical index called Yule's association coefficient. We then asked whether there was more coordination within subgroups than between subgroups. For instance, did wasps within a subgroup 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 among themselves also had a positive association coefficient, 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 subgroups well before the fission, with the Loyalists and Rebels behaving as two coordinated subgroups and avoiding each other. The wasps must therefore have been capable of individual recognition and must 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 the identity of successors to ousted queens. The behavior of two of the wasps was particularly interesting. Red was very aggressive, and particularly so toward 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 was not only trying to avoid Red but also trying to appease the queen.

The most dramatic example of this occurred one day when Blue returned to the colony with food but before she could land on the nest, Red noticed her 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 centimeters away from the nest, something that returning foragers seldom do—they usually 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 made several attempts to get on the nest but Red always blocked her way and tried to grab the food. Having failed to attract the attention of the queen or to climb 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 in light of what happened 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 in the colony for over a month after Blue took over, but I cannot help describing her behavior 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 much more aggressive toward Blue than toward other individuals? Why was the queen so "considerate"of Blue? Was there some kind of alliance between Blue and the queen? If so, did it have any influence on Blue's becoming the next queen when I removed the original queen, even though Red was higher in the dominance hierarchy?

Do Wasp Workers Choose Their Queens?

During a similar queen-removal experiment with *Ropalidia 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 March 9, 1985, Blue took over the place of the queen and Orange promptly left the colony. Blue, however, was apparently 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 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, since no wasp would supply 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 to the nest, 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 March 20, Orange returned for good and Blue left. A pity that I was not there to witness their meeting! Now the behavior 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

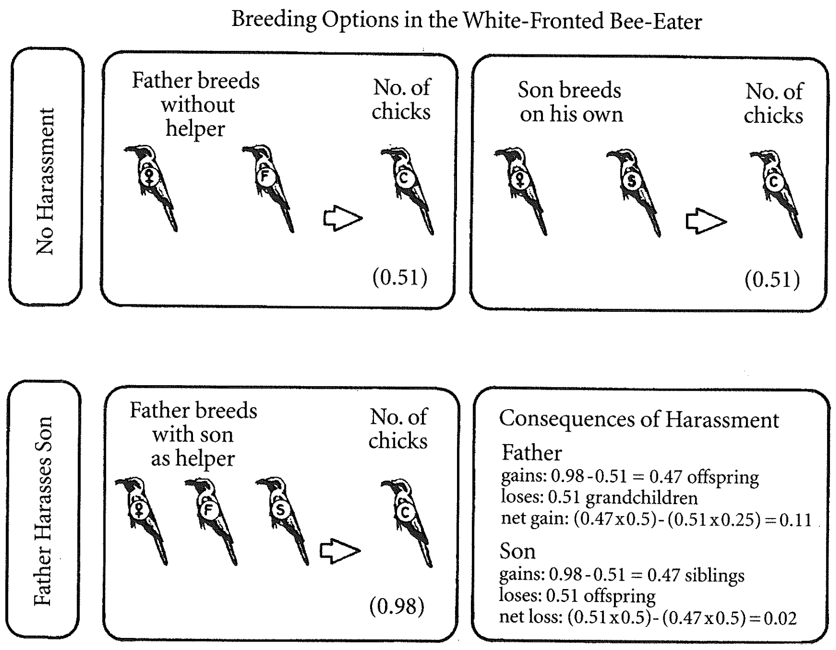
quite left the nest. She would also come from time to time and visit, as if to see how her rival, Orange, was doing. After a few days Blue decided to rejoin the nest, but not before experiencing a great deal of hostility from the resident wasps. Blue had to spend nearly a whole day being subordinated by several residents before she was accepted back into the colony. Once again, we see that wasps can recognize individuals, and it also appears that they can modify their behavior based on that 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?

Paternal Harassment of Sons in the White-Fronted Bee-Eater

Let us return to the study of the white-fronted bee-eater discussed earlier in Chapter 6. Emlen and Wrege saw white-fronted bee eaters engage in a bizarre kind of conflict. Some individuals, particularly adult males, harassed other members of their clan, particularly their sons, and prevented them from starting their own families. Harassment included persistently chasing potential breeders away from their territories, interfering with their courtship by preventing them from feeding their consorts, and physically preventing potential breeders from entering their nests by blocking the nest entrances. A frequent consequence of such behavior was that the harassed individual abandoned its attempts to breed and returned to the harasser's nest to act as a helper. Why do adult males harass potential breeders in this fashion? Why do they seem to particularly choose their sons as targets of harassment? Why do the sons accede to such harassment and not resist it more firmly? Why is it that the adult males have the greatest success in recruiting helpers through harassment when they target their sons?

Amazing as it may seem, all these apparent paradoxes are understandable within the framework of inclusive fitness theory. Since Emlen and Wrege had all their bee-eaters marked and the fate of each nest recorded, they could compute the costs and benefits of harassing as well as of acceding to harassment. First let us look at harassment from the point of view of the adult males. What are the costs and benefits of harassing their sons? If harassment is successful, the sons will come back to the nest as helpers and increase the number of offspring that the adult males can produce. That is a benefit. But then the sons will not breed on their own and hence the harasser will lose some grandchildren. On the average, a nest without helpers—with the only adults being the breeding pair—produced 0.51 offspring, while a nest with one additional helper produced 0.98 offspring. Fathers who harass their sons and bring them back would gain 0.98 – 0.51 = 0.47 offspring and lose 0.51 grandchildren. Since 0.47 offspring are far more valuable than 0.51 grandchildren (remember the father is related to his offspring by 0.50 and to his grandchildren by only 0.25), natural selection should favor fathers who harass their sons.

But why does the son not resist? Let us now do the calculation from his point of view. A son who came back and helped his father would contribute to the production of 0.47 siblings and lose about the same number, 0.51, of offspring (that he might have produced on his own). Since he is equally related to his siblings and to his offspring (note that we are now dealing with a diploid system and a not a halpodiploid system, as occurs in the Hymenoptera), it does not matter too much to the son whether he helps or breeds. Thus natural selection on the son will not be very strong. The fathers will be selected to keep trying to get back their sons while sons will not be selected to resist too strongly.

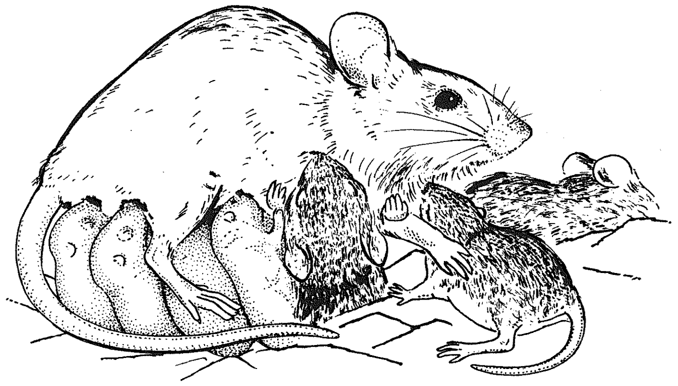


Breeding options in the white-fronted bee-eater. *(Based on Emlen and Wrege 1992; drawing by Sanjeeva Nayaka.)*

Communal Nursing in House Mice

House mice live in social units that typically consist of a single dominant male and one or more adult females with their offspring. The male mates with each female in his unit but provides no parental care to the pups. When there is more than one female in a reproductive unit, the females have abundant opportunities for cooperation and conflict, especially since they all litter at about the same time and rear their pups in a communal nest.

Barbara König at the University of Würzburg in Germany created monogynous and polygynous reproductive units in the laboratory to examine the balance between cooperation and conflict. On average, females in polygynous units fared better than those in monogynous units, especially if the females sharing a communal nest were sisters (sisterhood appears to be inferred by the mice on the basis of familiarity—a reasonable basis for such inference in nature, where sisters are likely to be familiar and nonsisters are likely to be unfamiliar). The main reason for the better performance of mothers rearing their pups in communal nests is that a given female suckles not only her own offspring but also those of her breeding partner—a behavior that human mothers would consider an extreme example of altruism. Perhaps even more striking to the biologist is the apparent inability of the females in a communal nest to discriminate between their own offspring and those of their partners, even when there is considerable age difference between their own and alien pups. Such communal nursing is observed even if the females living in a communal nest are unrelated and unfamiliar; clearly this is not merely another case of nepotism.



Communal nursing in house mice: mothers nurse their own pups along with other pups (of their breeding partners), which may have reached a significantly more advanced stage of development than their own pups. *(Drawing: S. Bonsani.)*

Females who nurse nonoffspring must gain something, and here is where the conflict comes in. The expression of conflict can be as dramatic as the expression of cooperation. Females who nest together do not litter at exactly the same time; their litters are usually separated by about 8 days. The female who litters later often kills one or two offspring of the female who litters first—the infanticide being committed here by females, whereas among the langurs it was always the males that were infanticidal. The probability of committing infanticide is higher if the female who has the opportunity to do so has a large litter inside her body—it appears that the mice have a way of assessing the litter size even before giving birth. Having killed one more of her partner's offspring, the female then litters and begins to nurse her own offspring and the remaining offspring of her partner indiscriminately, as if nothing unusual had happened. Production of milk is costly, and by killing one or two of her partner's offspring the infanticidal female causes increased flow of milk from the other female to her own offspring; obviously this is more important when her own litter is a large one.

Why does the second female not kill all the offspring of the first female and attempt to channel all her partner's milk to her own offspring? It appears that if the first female loses all her offspring she will cease to produce milk, and it would therefore not be prudent on the part of the second female to kill all the first female's offspring. Why don't females nest alone and avoid having their offspring killed in this fashion? Barbara König's experiments show convincingly that monogynous females produce fewer offspring than each member of the polygynous pair. The female who litters first and perhaps loses some of her offspring through infanticide by her partner will probably be the second to litter next time around, and will then be able to pay her partner back in the same coin. When you compute their lifetime reproductive success, the two females more or less break even with each other but both do better than monogynous females. By killing some and suckling some of their partner's offspring, by a mix of cooperation and conflict, these females achieve higher fitness than do solitary mothers. This example illustrates rather strikingly that you can rarely have cooperation without some conflict or conflict without some cooperation. Both cooperation and conflict are inevitable consequences of social life, and they are often inseparable components of a survival strategy.

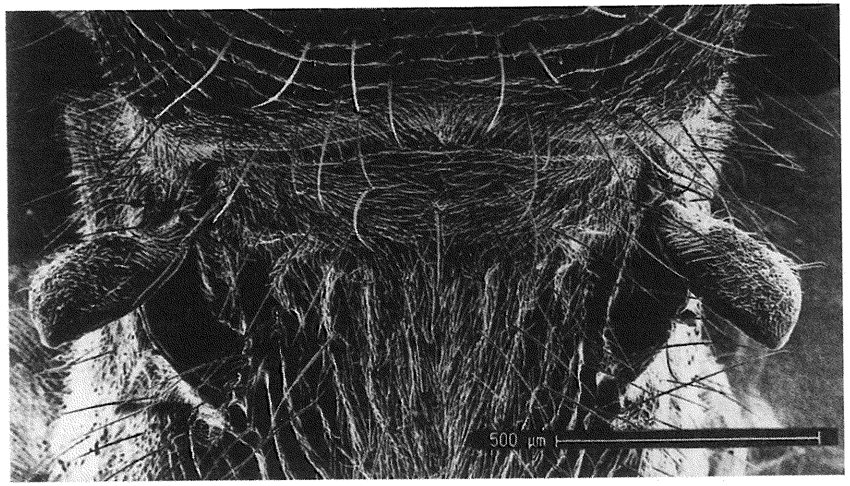
When Ant Queens Mutilate Workers

Diacamma is a rather unusual ant. It lives in societies with a single reproductive that we might call the queen, with the remaining ants acting as workers with a fine division of labor. Since ants usually have a morphologically well differentiated queen, we can tell from observation that such a true queen does not exist in *Diacamma*. It appears that the workers have simply stopped producing queens and have learned to manage on their own. This is a group of ants where the workers have not lost the ability to mate and store sperm. So the workers can indeed manage on their own. In a way, then, these ant colonies are like my *Ropalidia* colonies, where one of the many nearly identical individuals assumes the role of a queen.

Christian Peeters and his colleagues carefully examined such queens (whom they called gamergates, to distinguish them from the morphologically differentiated true queens of other ants) and workers from species of *Diacamma* from southeast Asia and Australia, and found that the gamergates and workers are morphologically different after all. The gamergates have little wing buds called gemmae (ant workers do not

A typical nest mound of the queenless ant *Diacamma ceylonense* in the Indian Institute of Science, Bangalore. *(Photo: K. Kunte.)*

have wings), while the workers don't have gemmae. But what makes *Diacamma* remarkable is what happens after the ants are born—a colloquial expression for emerging from the pupal case; an insect should perhaps be said to be born twice, once when the egg is laid and again when it completes metamorphosis and emerges as a completely transformed individual from its pupal case. All individuals are born with their gemmae intact, but the gemmae of all the ants are physically and violently mutilated by the queen. If the queen dies, the first ant to emerge subsequently retains her gemmae because there is no one to



Scanning electron micrograph of *Diacamma australe* showing the thoracic appendages called gemmae. *(Reproduced with the permission of Springer-Verlag from C. Peeters and S. Higashi, "Reproductive Dominance Controlled by Mutilation in the Queenless Ant Diacamma australe," Naturwissenschaften, 76 [1989]: 178.)*

remove them, and she then systematically mutilates the gemmae of all who emerge after her. The gemmae are required for mating, probably because they send chemical signals to the males. Ants without gemmae are characteristically mild and submissive and workerlike, while ants with gemmae are dominant and aggressive and characteristically queenlike.

Nobody knows how the presence or absence of gemmae affects the behavior of the ants, but here is a system where queens maintain their status as the sole reproductive of the colony and suppress all other individuals by mutilating them. The system is so designed that if the gamergate dies accidentally, the next individual to emerge will automatically become the next gamergate. The workers who have had their gemmae mutilated appear to work efficiently for their colonies without any trace of discord, and may actually be selected by natural selection to do so owing to the indirect social component of inclusive fitness that they get by rearing the gamergate's offspring. Nevertheless, it is evident that conflict is the flip side of cooperation is evident from the fact that the "queens" have to mutilate workers to get them to work.

When Ant Workers Kill Queens

Solenopsis is a small ant with a very painful sting. If you accidentally step on one of its nest openings, you will soon have hundreds of ants crawling over you and biting you. You will soon feel that your body is on fire, and you will understand why these creatures are called fire ants. One species, *Solenopsis invicta,* occurs naturally in Argentina and has been accidentally introduced into North America. As a recent introduction, it has few or no enemies in the new habitat and is rapidly spreading across the southern United States. North Americans seem to consider the fire ant a serious pest and are pouring huge amounts of money into fire ant research. I have no complaints because this has resulted in some of the finest research into ant biology.

Kenneth Ross at the University of Georgia and a visiting scientist from Switzerland, Laurent Keller, have recently uncovered a fascinating aspect of the fire ant story. Some colonies have a single queen while others have many queens. Being monogynous or polygynous appears to be a matter of tradition (if wasps can indulge in politics, why can't ants have tradition?); monogynous colonies rear big fat queens, suitable for starting new monogynous colonies, while polygynous colonies rear small queens, suitable only for entering and surviving in other polygynous colonies. In polygynous colonies, workers seem to limit the food given to maturing queens and if they encounter a really strong queen (some queens appear to be capable of becoming strong and dominant by virtue of their genetic make-up), they kill her and thereby ensure that a single dominant queen does not bully all other queens into submission and convert the colony into a virtually monogynous one. Thus polygynous colonies cannot turn monogynous because their polygynous state is perpetuated by the workers, who will not let a single queen dominate. For this reason Ross and Keller have described polygyny in *Solenopsis* as a "culturally" transmitted character, one passed on from one generation to another irrespective of the genetic make-up of the queens that enter an already polygynous colony.

Who's the Boss?

In most highly developed ant and honey bee colonies, the queen normally produces one or more chemical substances, called pheromones, that are meant to suppress the workers and prevent them from developing their ovaries and laying eggs. This quite naturally suggests that the queen controls the workers for selfish reasons and that the workers are forced to behave in an apparently altruistic manner. We then go on to explain that the workers' altruism is not eliminated by natural selection if they gain sufficient inclusive fitness by rearing the queen's offspring, who may be their relatives. But this also means that the worker is acting selfishly by preferring to be a sterile worker rather than going off on her own to start a new nest because staying gives her more inclusive fitness than leaving. So who's the boss in the ant or bee colony? Is the queen controlling the workers or are they staying "voluntarily"? This is not just a matter of semantics. We cannot define the function of the queen pheromones until we decide who's the boss. All along, we have thought of the queen as the boss and regarded the queen pheromones as worker-controlling substances.

Laurent Keller and Peter Nonacs have recently challenged this view and argued that we must think of the queen pheromones not as substances meant to control the workers but as signals used by the workers to voluntarily curtail their own reproduction because they are better off if the queen reproduces. One interpretation is that the workers are prevented by the queen from reproducing and that in her absence this inhibition is removed and they start reproducing. A different interpretation is that the workers prefer having the queen reproduce rather than doing so themselves because the queen is so much better at it. But if the queen dies, it is better for them to reproduce than for nobody to do so. Hence they use the queen pheromones as a signal to decide whether they should let the queen continue to lay eggs or whether they should do so themselves. So who's the boss? Perhaps the question is a pointless one, after all. From the point of view of natural selection, there is no boss; each individual is attempting to maximize its own inclusive fitness and the net result is that there is always a precarious balance between cooperation and conflict.

Little wonder then that the fine balance between cooperation and conflict is ubiquitous. Although slime mold amoebae are willing to commit suicide to enable some of them to disperse, they are always ready to cheat if some of the members of the group are genetically unrelated. Both parents of the blue tit family are willing to feed the chicks in apparent harmony, but the male is always ready to quit after bringing up a few strong chicks and the female has her own way of ensuring his continued cooperation by making all chicks the same age and size. Worker ants and bees spend their whole life caring for the queen's offspring but will try to feed their sisters more food than their brothers. Worker honey bees will try to sneak in their own sons in place of brothers, but the queen retaliates, creating discord among the workers by ensuring that they are only half sisters. Queen bumble bees will even make their daughter workers more susceptible to disease if that's what it takes to ensure their prolonged cooperation. Queens will mutilate workers and workers will kill queens if that's what it takes to ensure "harmonious" social life.

I have endeavored to show that both cooperation and conflict are inevitable consequences of the survival strategies of social animals and that a common theoretical framework can be developed to explain the observed mix of cooperation and conflict in different situations, whether we are dealing with slime molds or with chimpanzees. The examples I have chosen are my favorites, but cooperation and conflict are endemic in all animal societies.

10

Some Caveats and Conclusions

The Power of Simplifying Assumptions

A point that I have emphasized right from the beginning is that physiologists and evolutionary biologists should not quarrel about whose explanation is more correct. If the physiologist finds that birds migrate because their pineal gland has detected changes in day length and the evolutionary biologist finds that the cost of migration is less than the cost of having to spend the winter in the northern latitudes, both are correct because they are dealing with two different levels of explanation. It does not make sense to try to decide which of the two explanations is better. Much unnecessary debate and confusion is avoided if we recognize the distinctness of the two different levels of analysis and work within either one of them. Ignoring the possible physiological explanations and focusing on the evolutionary explanation or vice versa appears to be a legitimate way of avoiding confusion. It is also sometimes inevitable because the training and methodology and quite often the very philosophy of scientific research underlying the physiological and evolutionary explanations may be quite distinct. But the time must come in